Ecological and Economic Entomology

A Global Synthesis

B. E. Freeman

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1 General Introduction

> If the karate-ka (student) shall walk the true path, first he will cast aside all preference.
>
> Tatsuo Shimabuku, Grand Master of Isshin-ryu Karate

1.1 The Importance of Insects

Because of their great numbers and diversity, insects have a considerable impact on human life and industry, particularly away from cities and in the tropics. On the positive side they form a large and irreplaceable part of the ecosystem, especially as pollinators of fruit and vegetable crops and, of course, many wild plants (Section **8.2.1**). They also have a place in soil formation (Section **8.2.4**) and are being used increasingly in 'greener' methods of pest control. Biological control using insects as predators and parasites of pest insects has been developed in the West for over a century, and much longer in China. More recently *integrated pest management* (IPM) and *conservation biological control* (CBC) are being deployed to better effect.

Entomology has played a major role in the development of ecology and other branches of biology such as genetics, physiology and behaviour. This is not only because insects form the major part of the terrestrial fauna, but also because they offer a convenient method of study. Their relatively small size leads to easy handling and their abundance facilitates sampling and, in turn, a numerical analysis of the results. Their main disadvantage is that there are too many of them. So many orders, families and species exist that learning about their immense diversity takes a long time and not inconsiderable effort. Also, many people are entomophobic: they just do not like insects and proceed in ignorance to belittle their far-reaching effects on people and the environment. After you read this book you will not be among them.

But of course, some insects have a negative side, and in a few this side is considerable. Before harvest they, together with weeds and pathogens, destroy ~30% of the plants we grow for food and materials. Insects transmit some of these pathogens. While weeds can often reduce pest attack, they can also harbour the pest's enemies or provide alternative resources for the pest itself. Then in storage, insects, mites, rodents and fungi cause a further 30% loss. Apart from such biotic damage, severe physical conditions such as drought, storms and flooding cause additional losses. For example, under ideal field conditions new wheat varieties (e.g. Agnote and Humber) would give yields of ~16 tonnes/ha, but produce typically about half this under good husbandry. Pre-harvest destruction due only to insects is 10–13% (Pimentel *et al.*, 1984; Thacker, 2002). Losses are probably higher in the Developing World. Hill (1997) and Boyer *et al.* (2012) estimate 30–40% of total crop losses globally. Polis (1999) states 'Worldwide, ... insects take about as much crop production as is used by humans', although other data (Reynolds, 2012a) suggest that this estimate is too high. But without crop protection, chemicals included, losses could be 30% higher than they are with it (Oerke, 2006). Over the years there has been a shift of expenditure – insects now cost us large amounts for crop protection, hopefully to lessen their effect. The annual bill for agricultural insecticides is now approximately US$7 billion in North America, and more than US$20 billion worldwide. Even so, their effectiveness is variable. Naturally, these estimates are but a fraction of the total because the costs of application and wasted time should also be put on the account.

This situation has promoted a huge research effort, but since agriculture in its widest sense is the world's biggest productive industry, and since research scientists are, in the main, dedicated people working

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for low salaries, generally this has been cost effective. A Premiership footballer gets twice as much in a week as the average scientist gets in a year. Hopefully, future generations will wonder at this past stupidity. One of the reasons why improving pest control is critical, is that although new crop varieties have greatly increased production (Oerke, 2006), traditional crops had more innate resistance to insect damage. Traditional rice in Asia had losses of only a few per cent, while modern varieties can have losses around 25%. Even so, they produce five times as much grain per hectare and that is the bottom line; a basic principle.

The widespread use of insecticides, fungicides and weed killers has brought environmental pollution in its train. Conversely, in traditional African agriculture little is spent on chemicals, but losses from pests are very apparent. Environmental degradation in Africa is due largely to deforestation; in Europe that has happened already. Only if we can learn to manipulate our environment and agro-ecosystems in particular in permanent ways, with low recurrent expenditure, would we have defeated enemy insects. This has been achieved in a few cases. But ‘permanent’ is euphemistic when applied to biological systems: the playing field is uneven and the rules partly known. While limits exist (Arnold, 1992), evolution works constantly (Haldane, 1954; Trivers, 1985), adjusting the positions of all the living players.

Progress in our favour has continued for several decades, but an idyllic *final solution* is still far off. Old organic insecticides such as DDT were applied at an average rate of 1 kg/ha; now alpha-cypermethrin is applied at around 10 g/ha. These developments come not only within the ambits of organic chemistry, ecology, largely applied ecological entomology and population dynamics (Berryman, 1991b), but also those of economics and management. And any system used to combat insects must dovetail into the control of other pests, agricultural practice in general and into economics. The nearest to the ideal solution we have come are biological control and IPM, but these methods do not always work and there may still be an environmental backlash (Pimentel *et al*., 1984). Related techniques of landscape management and CBC are still being developed. But ignorance, lack of aesthetic awareness and avarice continue to be important social factors.

Insects attack not only our field, forest and orchard crops, but also our domesticated animals and ourselves, making it more difficult for us to practise agriculture. There are direct and indirect effects. Both farmers and livestock may suffer insect bites, become victims to their juvenile stages or get infected with insect-borne diseases such as malaria and dengue. As we will see, only a few insect species are pests; most are beneficial. The number of important pests is around 0.1% of the vast number of described insect species (about 1000–2000 species in total). With time, some species gain and others recede in their importance. This is because new crops are developed and grown and new forms of husbandry are devised, but also because agro-chemicals are misused. Insects also migrate and/or change under climatic and evolutionary influences, while management is rarely fully informed.

1.2 Insect Size

In the scale of life, insects are of small to medium size. Mymarid wasps that parasitize insect eggs weigh <1 mg, while at the other end of the scale Goliath beetles may attain 40 g, a range >40,000 mg. Hamilton (1996, p. 386) provides an even greater range: *Titanus giganteus* from palm logs in Brazil are a million times bigger than ptilinid beetles (*Ptinella*). Their size relative to other terrestrial animals, their size within the range for insects and even their own species have basic consequences for their physiology and ecology (Price, P.W., 1997). We hear fables of fleas scaled to the weight of a man jumping over famous public buildings. This nonsense is the result of a naïve linear scaling of both weight and power. But weight is a cubic function of body length, whereas muscular power is only a squared function. Doubling in weight produces much less than doubling in power. Small size also allows insects to exploit the great physical variation in their environments (Section **10.1.1**). Another critical effect is that the smaller the organism, the greater its surface area (a squared function) relative to its weight. Big animals are in the grip of gravity, little ones are more affected by surface effects. Small insects trapped in a film of water may be unable to free themselves. These relationships give us a glimpse into the foreign physical environment of the insect, for example, how a fly can land upside down on a ceiling.

The world is relatively a much larger place for a small animal than it is for a large one (Hutchinson, 1959; Morse *et al*., 1985). To continue with insect size discussion, our mymarid wasp develops within the minute confines of a moth’s egg, but the larva of the big moth *Manduca sexta* may have to eat an entire tomato plant for development. Many phytophagous insects live inside their plant food (*endophytic*). Some cereal beetles can live out their juvenile lives within single grains. Indeed, the rather low metabolic rate of larval forms allows them to survive in cryptic places. Here oxygen is deficient, but they avoid desiccation and predation. Several moth caterpillars, like the teak defoliator (Section **5.2.1.4(k)**), roll up leaves and hide therein, and several species pupate in them or use a small chink in the bark of a tree. The small size of insects in general means that their environment, and especially their hygrothermal environment, is very patchy.

Again because of the physics of scaling, flight is an efficient mode of locomotion for insects (Ellington, 1991; Harrison and Roberts, 2000); we need think only of the prodigious distances covered by migrating butterflies like *Vanessa cardui* (Section **12.3.3.2**). While the *rate* of energy consumption in flight is much greater than that of crawling, the *total energetic cost/km* is far less (Kammer and Heinrich, 1978). This is partly due to the physics of flight, but also includes wind assistance and avoidance of obstructions on the ground. This is critical for small insects due to the effect of size on the fractal nature of their world, they can take only small steps on the ground (Section **12.2.6**). The evolution of mobility in most adult insects alters their spatial ecology relative to that of their juveniles *and to all other terrestrial invertebrates* (Section **12.3.4.4(c)**). It allows them to migrate, seek resources and control landing, and so are able to exploit fully the three-dimensional nature of their habitat (Roff, 1990; Marden, 2000), attributes extending back more than 350 million years ago (Ma). Flight has continued to evolve over this immense period, allowing longer migration and increasingly sophisticated resource seeking (Section **10.2.4.1**). Vagrant insects may migrate >500 km in a single generation. The inception of flight brought about a refinement in *risk/reward dynamics* (q.v.; means *which see*, refer to Glossary throughout text) and mitigates the changing heterogeneity of the environment. While parasitic worms produce huge numbers of eggs and larvae that seek new hosts, these are earth bound. Aphids and fruit flies fly aloft, greatly extending their area of environmental scanning.

But to fly an insect requires >12% of its body mass in flight muscle. Since muscle is metabolically expensive to build and maintain, there is often a trade-off between flight and reproductive capability (Zera and Denno, 1997; Marden, 2000). Insect size affects both mobility and reproduction. Insect flight muscle is of two types: the *synchronous* or *neurogenic* type in which each neural stimulus produces a single contraction; and the *asynchronous* or *myogenic* type in which it produces multiple contractions. Unsurprisingly, wing-beat frequency, wing loading, mass-specific power output and fuel consumption are usually greater in the latter. While insect flight mechanisms have similarities to those of birds, their wings have no intrinsic muscles so changes in wing shape are controlled by structural mechanisms. Indeed, *controlled deformability* is the essence of insect wing design and function; they are elegantly adapted flexible aerofoils (Wootton, 1992).

Insect shape is another consideration, especially in relation to hygrothermal control. Compact insects like higher Diptera and many beetles have less body surface for a given mass than elongate ones, such as dragonflies, locusts and crane flies. The latter potentially desiccate more easily and some are more affected in flight by wind (Freeman and Adams, 1972). But elongate insects like grasshoppers and asilid flies are better at using differential orientation to gain or lose heat as the situation demands (May, 1979; Morgan and Shelly, 1988; see also Section **10.1.1**). When too cool they orientate to cast a big shadow, or when too hot cast a small one, or even take a position in the shade of a grass stem. In some Orthoptera such as *Schistocerca* and *Orphulella*, the thorax is flattened ventrally and can be pressed down on warm ground, therefore gaining free heat.

The high metabolic rate of most adult insects contrasts them with nearly all other terrestrial invertebrates, and is a consequence of their efficient system of gaseous exchange: oxygen in and carbon dioxide out. Their unique tracheal system of fine air tubes, assisted in active insects by ventilated air sacs, permits rapid gaseous exchange (Price, P.W., 1997; Dudley, 2000; Harrison and Roberts, 2000). Even simple diffusion of oxygen down tracheae is very much faster than it would be through tissue. Compared to vertebrate blood systems, tracheal systems are light, promoting a higher power : mass ratio. Muscular vibration also assists respiratory exchange, and differences in pressure between the front and back of some flying insects, the *Bernoulli entrainment*, can pull gases through them. Insect metabolism is unconstrained by a lack of oxygen if they have access to air. Indeed the flight muscle of euglossine bees (Section **8.3.6**) is the most active tissue known (Casey *et al.*, 1985; Dudley, 1995).

All flight muscles are liberally supplied with mitochondria (Marden, 2000), but inactive insects consume little oxygen, while during inclement seasons, insects frequently enter a hormonally mediated state of low metabolic activity and morphogenesis (Tauber and Tauber, 1981) called *diapause* (Section **10.2.3**).

1.3 Insect Taxonomy in Relation to Physiology and Ecology

While physiology and ecology relate to insect size, they also relate to insect classification, but of course for entirely different reasons. First, the basic split into exopterygotes and endopterygotes (Section **1.4**) has important ecological consequences. The lack of a pupa in the former group means that there is, for terrestrial species at least, no fundamental change in lifestyle between the juvenile and the adult. The degree of transformation of a squirming maggot in a carcass to a fast-flying adult blow fly would be impossible in an exopterygote, although in the palaeopteroid orders (Section **1.4**) changes between an aquatic nymph and a flying adult are very marked. Therefore in the Odonata, nymphs are modified as aquatic predators and adults as aerial ones. Again, most endopterygotes suffer from having two, non-feeding immobile stages (i.e. egg and pupa) that possess only passive or physiological defences (Danks, 2007). Behavioural defences that depend on movement are debarred (Section **10.1**). Second, insects in certain groups are specialized towards particular lifestyles. Herbivory is found mainly in the six largest orders (Section **2.3.1**), suggesting that the habit itself has promoted speciation (Section **9.10**). Numerous Heteroptera are terrestrial or aquatic predators. The Lepidoptera are mainly herbivorous. Female Hymenoptera, apart from phytophagous sawflies, are largely predators and parasitoids (Schoenly, 1990), which is regarded as a consequence of their evolving a sting. But many Diptera and Coleoptera are similarly aggressive towards other insects. Lifestyle, to an extent, is linked to taxonomy.

1.4 Learning Insect Classification

Because insects are so numerous and so diverse, a competent economic entomologist must be, at the outset, a competent general entomologist. For the beginner this is a daunting prospect. It means being able to recognize living insects on sight as far as the group to which they belong, and to know the essentials of their biology. After that, one must use appropriate taxonomic keys. An applied entomologist would be worse than incompetent if he/she could not separate, for example, a predatory carabid beetle from a wood-feeding tenebrionid beetle or a leaf-eating chrysomelid beetle. Misidentification can lead to inappropriate action, which is generally worse than no action at all. But the level to which identification should go varies – it may be adequate to recognize a family in some circumstances, but on others one must identify the genus or the species. Now, as we noted, there are an awful lot of insect species. Over a million have been described. They are arranged in ~30 *orders* and ~1000 *families*, each with its own special morphological and often ecological characteristics. When all insect species are described, and we have a long way to go, there will be several million of them, maybe more (Hammond, 1992; Dudley, 2000; Reynolds, 2011). But while Hutchinson (1953) mused on the great abundance of species, Felsenstein (1981) inquired, given the dynamics of speciation (Section **9.10**), why there are not even more.

Although this book is not general entomology, in order to get the most out of it some familiarity with insect classification and biology is essential. We will refer to many insect species by scientific name: many plant pests, vectors of disease, predators and parasitoids, for example. They are named as a reference and to give beginning students a glimpse at their enormous diversity. You do not have to learn them all! (Forthwith I will usually lapse the term ‘beginning students’ to just ‘students’, still implying the possibly fortunate young, but also recognizing that we are all still learning.) I provide here some guidelines as to how familiarity with insect classification may be achieved without undue pain, a familiarity that does not breed contempt. These guidelines should be used in conjunction with some comprehensive textbooks.

There are two traditional textbooks in English. *Imms’ General Textbook of Entomology*, revised by O.W. Richards and R.G. Davies in 1988, is an imposing two volumes (we quote books by the names of their authors, not by their titles). This work is better for the European and Old World insect fauna. Then there is Borror and DeLong, which has been revised by C.A. Triplehorn and N.F. Johnson successively (Triplehorn and Johnson, 2005). This work is directed towards North American insects and is replete with excellent illustrations, combining simplicity with accuracy. Both books, however, are completely comprehensive. The classifications they use are substantially the same, although they differ in some particulars. While Richards and Davies' revision is a bit dated it is more detailed. Owain Richards was a man of encyclopaedic knowledge of insects and ecology. He once told me in a rare moment of levity that since retirement he no longer worked 18 hours a day. 'Only twelve', his wife added. He used his time efficiently, never greeting you normally, and with no preface of pleasantries he would continue straight into the previous scientific conversation that you had been having, adding new information and perspective. Quite an intellectual ordeal when I was young. Also worth delving into is J.H. Comstock's (1940) *An Introduction to Entomology*, which went into at least nine editions, and bears the author's austere portrait at the front.

Recently, Gillott's (2005) comprehensive text has gone into its third edition. Then there are Arnett's (1985) handbook of American insects, Chapman's (1998) textbook on the general structure and physiology of insects, Daly *et al.*'s (1998) work, which contains a section on systematics and biology, and Grimaldi and Engel (2005). There is also an insect encyclopaedia edited by Resh and Cardé (2003). Several books exist that cover only a single insect order, such as Dolling (1991) on the Hemiptera, Gauld and Bolton (1991), Austin and Dowton (2000) on the Hymenoptera, Ford (1955) on moths and Oldroyd (1964) on Diptera.

When I was taught entomology at university we started at Order 1, the Thysanura, and ended up at Order 29, the Strepsiptera. This was the wrong way to do it. It was rather like a temporal version of Columbus' first voyage to the Americas. It is said that when he went he did not know where he was going; when he arrived he did not know where he was; when he got back he did not know where he had been; and he did it all on public money. So that this does not happen to beginning students I provide the scheme which now follows.

The scheme consists essentially of looking at insect classification in plan; you see all the essentials together. One learns the most important things first, the lesser things subsequently and, like a Google map, zoom in progressively on layers of increasing detail. But before starting we put the primitively wingless insects, the sub-class Apterygota dating from the Lower Devonian Rhynie chert some 400 Ma, to one side. We are left with the vast majority of insects, the sub-class Pterygota, or 'winged ones', which arose somewhat later (Scott *et al*., 1992). Next, it is cardinally important to remember that the Pterygota come in two quite different sorts, a difference that is based on the type of development from egg to adult.

Like all arthropods, insects have a dead external skeleton (exoskeleton) functioning for support and protection. It comprises diverse proteins, contains chitin fibrils and is surmounted by a protective epicuticle. Complex structural interplay between the protein and chitin components gives the cuticle diverse properties of physical protection and flexibility, as in other composite materials such as fibreglass. But since the exoskeleton is *dead* it has to be *shed* periodically, permitting the insect to grow and develop, like a young medieval prince having to be fitted annually with a new suit of armour as he grows into a man. Insect growth is cast into a series of stages, or *instars*, between sheddings. Apart from elaborate organs such as antennae, and compound eyes that can see *everywhere at once*, insects perceive the external world with a complex array of sensory hairs passing through this armour; as Taylor and Krapp (2008) put it: they 'bristle with sensors'.

In some insects the wings develop gradually on the outside as four increasingly visible buds as the individual passes from instar to instar. They are hence called Exopterygota ('outside-winged ones') or Hemimetabola. They have been on Earth since the Upper Carboniferous over 300 Ma, although several orders, such as the Palaeodictyoptera, have become extinct (Labandeira and Sepkoski, 1993). In the Exopterygota, we shall call the stage that comes out of the egg a *nymph*. It usually looks something like a miniature, wingless adult and as it moults successively it gets to look more and more like a wingless adult. In the final moult the wing-buds expand so forming two pairs of wings and it *is* an adult. It does not moult any more.

Then there is the other, much larger group in which the wings develop on the inside of the juvenile stages, so that they are at first invisible externally. They are, hence, called the Endopterygota ('inside-winged ones') or Holometabola. Endopterygote orders are more recent, arising about 260 Ma in the Permian, and more recently have expanded in numbers in concert with the increasing diversity of flowering plants, although this is not the only factor in their success (Labandeira and Sepkoski, 1993). The creature hatching from the egg (*eclosion*) looks nothing like an adult and each time it moults it does not get to look any more like an adult, just bigger.

It is a *larva*, a specialized feeding stage. A *stage of change*, the normally sedentary *pupa*, has evolved allowing this stage to change into an adult. The adult, which *emerges* from the pupa, is the stage modified for dispersal and reproduction, usually in that order. It does not moult any more either.

Insect stages differ in mobility. These differences, while simple, are fundamental to their ecology. All eggs and endopterygote pupae are sedentary (unusual pupae will be noted later). All nymphs and larvae can move to a variable extent, although a few, like maggots and many boring beetle larvae, lack legs. Most adult insects have wings and can fly, although a few, like ectoparasitic fleas and lice, do not and therefore cannot. Here the term '*immobile stages*' refers to eggs and pupae, while '*mobile stages*' are the rest, although adult scale insects become anchored to their plant food. Thus, the ecology and population dynamics of insects change successively as they develop from egg to adult. Following this, the dynamics of endopterygotes are often more complex than are those of exopterygotes as there are four, not three, different life stages. Also, larvae are more different anatomically from adults than are nymphs from adults, and generally live in different microenvironments. The exopterygote orders Odonata and Thysanoptera (thrips) are particular exceptions. The former (Section **1.3**) comprises aquatic predators as juveniles and aerial predators as adults, and hence occupy very different media. Thrips usually start life as concealed eggs, feed on plants as active nymphs and then become quiescent in the soil before the dispersive adult develops. In both cases their enemies are different in each phase, adding complexity to their dynamics (Lewis, 1997).

1.4.1 Adult insects

Within this great sub-class Pterygota there are only seven groups that one must learn in order to navigate insect classification. These are placed in what I call the '*four-square diagram*' (**Fig. 1.1**). Vertically, the diagram divides the Pterygota according to whether they are exopterygotes or endopterygotes. Horizontally, it divides them according to the type of adult mouthparts. These are either the more primitive, biting or mandibulate sort, or the more advanced, sucking sort that evolved from them (q.v.). This horizontal split according to mouthparts is useful because it gives an entomologist a clue as to what type of insect did the observed damage to a crop plant, when, as is often the case, the culprit is no longer around to be identified. Sucking insects often transmit pathogenic micro-organisms (I will often use the shorter term '*microbes*'), both of animals and plants. Biters variously chew bits out of the plant, damaging the cells and releasing *elicitor* compounds (Section **2.4.2**), but rarely transmit plant pathogens. When a leaf is damaged, the bits removed relate to the size and behaviour of the biter, producing diagnostic patterns. Those of two teak defoliators, *Hyblaea* and *Eutectona*, are quite different (Nair, 2007). Suckers also have a variety of feeding mechanisms (Mitchell, 2004). The Heteroptera (larger) often damage tissue while feeding, leaving diagnostic spots, blemishes and

	BITING	SUCKING
EXOPTERYGOTA	Palaeopteroids Orthopteroids	Hemipteroids (Heteroptera, Auchenorrhyncha, Sternorrhyncha)
ENDOPTERYGOTA	Hymenoptera Coleoptera	Lepidoptera Diptera

Fig. 1.1. The four-square diagram. This is all one needs to learn about insect classification at first. Once it is off pat you have a map of the insect world, *continent by continent*, so to speak. As you learn about other insect groups, the smaller orders, sub-orders and large families, you place them in this framework. For example, the order Trichoptera (caddisflies) belongs at the vertical division of the endopterygotes. These insects are a bit like moths (sucking mouthparts) but have biting mouthparts. This is like putting *countries* into the *continents.* The Hemiptera were formerly divided into the Heteroptera and Homoptera, but the latter is now split into the Auchenorrhyncha and the Sternorrhyncha, which are each given sub-ordinal status. The former bugs are distinguished by having a terminal *arista* to the antenna, lacking in the latter. In the Sternorrhyncha the base of the rostrum arises between the fore coxae. In future, I refer to these groups jointly as *homopteroids*.

deformations at the site. They may lacerate cells (Lygaeidae), use pectinase to macerate them (Miridae) or employ salivary sucrase to induce osmotic unloading from the phloem (Coreidae) (Miles and Taylor, 1994). Many (smaller) homopteroids insinuate their mouthparts between the cells to seek vascular tissue (Howe and Jander, 2008). Sheath saliva is secreted along the stylet's path, and watery saliva at the feeding site contains a complex of enzymes (Kaloshian, 2004). While these bugs leave less obvious damage, the plant's tissue may deform and/or become chlorotic. They also transmit most plant viruses (380 species, 27 genera). The type of mouthpart also relates to other aspects of the insect's biology, which we will note in due course.

Recapping, the major phases in insect evolution are as follows (the arrows indicating increasing levels of sophistication):

Apterygota (Devonian) → Exopterygota (Carboniferous) → Neoptera (Upper Carboniferous) → Endopterygota (Permian)

1.4.2 Eggs and juvenile insects

Insect eggs are produced in paired *ovaries* within the abdomen. Each ovary consists of several tubular *ovarioles* in which eggs are produced in a linear chain. Highly fecund insects have many more ovarioles than do those with low fecundity, while larger conspecific females usually have more ovarioles than smaller ones. *Panoistic* ovaries lack nutritive cells, whose function in *meroistic* ovaries is to feed the eggs (Richards and Davies, 1988). The paired ducts from the ovaries join medially to form a vagina into which lead ducts from the *spermatheca* and various accessory glands. After copulation, sperm is stored in the spermatheca, sometimes for long periods. After fertilization, the accessory glands secrete diverse coverings to the eggs. The eggshell is termed the *chorion* and in harsh environments is complex and highly developed (Hinton, 1981). Fecundity may be measured as *maximum potential fecundity* (MPF) or *achieved fecundity* (AF).

But there is the question of identifying the juveniles. Nymphs and larvae also attack plants and animals, and one must know if they bite or suck. There are two simple rules. First, since exopterygotes have no pupa (the stage of change), adult and juvenile mouthparts *must* be rather similar. Exopterygote nymphs usually look and often behave like small, wingless versions of the adults. Second, all endopterygote larvae have biting mouthparts, although some are much modified. Larval Diptera Cyclorrhapha generally have rasping mouthparts, but adults have imbibing or piercing and sucking ones. Lepidopteran caterpillars have chewing mouthparts, but the adults usually suck nectar through a coiled proboscis. These stages have different feeding strategies and occupy different trophic levels. Biting stable flies are detritivores as larvae and micropredators as adults (Section **7.1.1.2**). One species occupies two trophic levels (Murdoch, 1966b). But we must grapple with the major types of endopterygote larvae. Luckily, there are only a few characters (Fig. 1.2).

Caterpillars of the Lepidoptera usually have several ocelli (simple eyes), three pairs of thoracic legs, four pairs of abdominal legs and a pair of terminal claspers. They have a complete head capsule with vertical jaws and a full set of spiracles. The main exceptions are caterpillars of the geometrid moths, which have a single pair of abdominal legs, and those of some blue butterflies (Lycaenidae) associated with ants, in which the legs are rudimentary. Sawfly caterpillars (Hymenoptera) are amazingly similar except for having only a single pair of ocelli, more than four pairs of abdominal legs (Section **5.2.1.3(b)**) and often an oily appearance. Beetle larvae are rather like caterpillars too, but they have no abdominal legs. The larvae of buprestid, cerambycid and curculionid beetles have no legs at all. This relates to their boring habit. Leglessness, in this instance, is a general feature of boring larvae.

Hymenopteran larvae, but not the sawfly caterpillars, are generally legless, move around only a little and have a full set of small spiracles. The head capsule is entire but often less heavily sclerotized than in beetles. They are usually either parasitic or in cells being tended by adult females. Dipteran larvae are always legless. They have a large pair of posterior spiracles facing backwards and looking a bit like eyes. The primitive larvae, as in crane flies and mosquitoes, have an entire head capsule with well-developed mandibles whatever their lifestyle. The advanced ones are *maggots*, in which most of the head capsule has disappeared and the mouthparts reduced to a pair of hook-like mandibles. For discussion of '*advanced larvae*', see McShea (1998).

Pupae are of course confined to the Endopterygota, and potentially vulnerable by reason of their immobility. But this stage can sometimes wriggle, warding

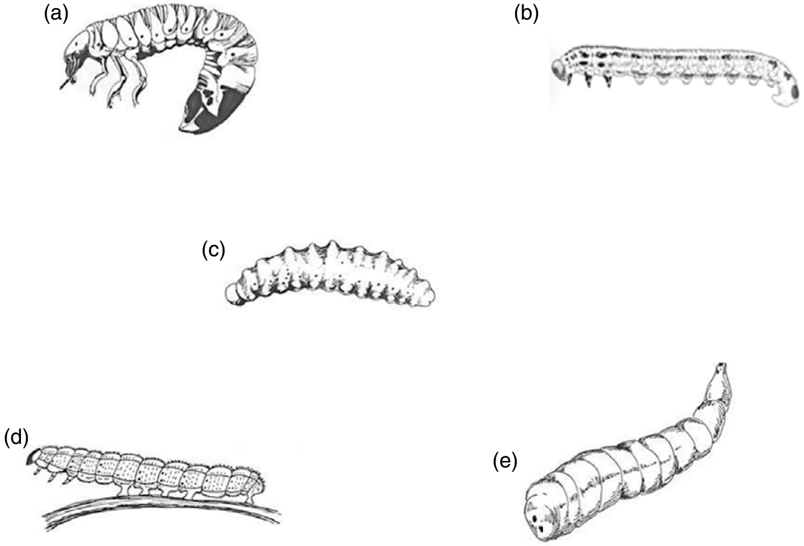

Fig. 1.2. To identify endopterygote larvae use the following simple features: (i) The presence or absence of legs. In the former case their distribution on the larva. Boring larvae tend to have lost their legs through evolution. (ii) The presence or absence of a complete head capsule. (iii) The distribution of the *spiracles* (breathing holes opening into the tracheal system). (iv) Orientation of the mandibles. Insects with horizontal jaws (*prognathy*) are often carnivores, those with vertical ones (*hypognathy*) are generally herbivores. Detritus feeders are variable. **(a)** Coleoptera. Thoracic legs only, robust head capsule, complete set of spiracles, mandibles prognathous (carnivores) or hypognathous (herbivores). **(b)** Hymenoptera, Symphyta. Thoracic legs and more than four pairs of abdominal legs, robust head capsule, complete set of spiracles, hypognathous. **(c)** Hymenoptera, Apocrita. Larvae enclosed in a host or cell, legs absent, head capsule present, complete set of spiracles, mandibles variable. **(d)** Lepidoptera. Thoracic legs and four or fewer pairs of abdominal legs, robust head capsule, complete set of spiracles, hypognathous. **(e)** Diptera. Legs absent, head capsule in Nematocera only, with generally prognathous mandibles. Spiracles prothoracic and terminal on the abdomen.

off attacks from parasitoids, or they are heavily sclerotized. Some braconid wasps pupate beneath or around their dead victims, for example, *Cotesia melanoscela* under gypsy moth larvae (Gross, 1993) and *Praon* spp. under aphids (Richards and Davies, 1988). Indeed, all ichneumonoid and moth pupae are protected both from desiccation and from enemies by a cocoon and sometimes by rolled up leaves. Butterfly pupae are exposed, but usually cryptically coloured (Section **1.5**). Those of other groups develop in hidden places: in the soil, in wood or in hollow stems.

1.4.3 Phenotypic plasticity and polymorphism

In populations of sexually breeding insects there is considerable *continuous* variation between the individuals of the same stage, that is, there are adaptive, individual differences between them (den Boer, 1968, 1998; Wilson 1998). First, individuals have different genetic structure resulting in different phenotypes. Second, a single genotype may exhibit variable phenotypes in different environments (Whitman and Agrawal, 2009). This is *phenotypic plasticity*. But there are many characters for which such variation is *discontinuous*. For example, adults of the ladybird beetle, *Adalia bipunctata*, may be black or red; there are no intermediates. Within several grasshopper species there are some adults that are mainly green and others that are mainly brown. In some parasitoids and water bugs there are short- and long-winged forms. Such *discontinuous variation* is called *polymorphism* and has been known for a long time (Reuter, 1875). Ford (1961) gives a good formal definition: 'Genetic polymorphism is the occurrence together in the same habitat of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained … by recurrent mutation'.

We add to Ford's definition only that the *same instar* must be specified. Essentially, variation is *intraspecific* and *discontinuous* (Harrison, 1980). A polymorphic population comprises morphologically distinct sub-units. All polymorphism has a genetic basis (Clark, 1976). Our definition excludes geographical races, continuous variation and rare mutants that are normally removed by natural selection. Analysis shows, however, that if a morph comprises as little as 1% of a population then it must have some selective advantage, often only when rare. In *A. bipunctata* the red forms survive the winter better, whereas the black forms have a higher rate of increase (r_m) during the summer. Mather (1955) showed that such polymorphism was the outcome of *disruptive selection* (q.v.).

Another conceptual angle on these different forms is metamorphosis itself. The same individual exists in different forms in *different instars*. Both polymorphism and metamorphosis (Section **1.5**) are, of course, adaptations for different functions, as Lubbock (1874) and Reuter (1875) noted in Darwin's time. Again with respect to time, there may be seasonal changes in morph frequency, as in adult *Adalia,* in some adult butterflies such as *Precis* (Mather, 1955), the tropical genus *Bicyclus* (Brakefield *et al.*, 1996) and in adult flies such as *Drosophila* (Birch, 1960). Two major polymorphic traits exist in insects: (i) colour and pattern polymorphism; and (ii) alary or flight polymorphism. For ecology, the first relates in particular to survival (Section **10.2.3**) but also to thermal relations, as in *Adalia*. The second relates to movement, in particular to redistribution (Section **10.2.4**). The latter affects: (i) variation in wing length; (ii) variation in flight muscle development; and (iii) variation in flight behaviour (Harrison, 1980).

Although polymorphism always has a genetic basis, in *genetically determined polymorphism* the environment has little or no modifying influence (Clark, 1976). In *environmentally cued polymorphism* or *polyphenism* (Mayr, 1963), the environment acts with the genotype to select alternative developmental pathways resulting in different morphs (Moran, 1992a). Polymorphisms are due to genetic differences between individuals. Polyphenic traits result from environmental differences acting on the same genotype, namely phenotypic plasticity. Such causal cues are commonly crowding, an intrapopulation effect, or temperature and food quality, which are factors of the wider environment. Crowding in the wasp *Melittobia,* and the ambient temperature during juvenile development in *Bicyclus* induces the change in adult forms (Section **10.2.2.2**).

1.4.4 Some further notes on insect classification

Several insect orders end in the suffix '*-ptera*', serving to identify their ordinal rank. Therefore the order Diptera comprises the 'two-winged ones' and the order Lepidoptera contains the 'scale-winged ones'. Unfortunately, sub-orders have no reliable endings to identify them, but all is not lost because next down the scale of classification, the superfamilies all end in '*-oidea*', the families all end in '*-idae*', the sub-families all end in '*-inae*' and the tribes, if they exist, end in '*-ini*'. Students must learn these suffixes, as I will not burden the text with explanations each time they turn up. They are also incorporated in adjectives, for example, pentatom*id* bugs, culic*ine* mosquitoes. In most plant families the equivalent ending is *-aceae*.

Species are given two names in international biology. For example, a common blow fly has the scientific name '*Calliphora erythrocephala*'. These names are always in Latinized form even if not actually in Latin. Contrary to popular belief, this practice was started not by Linnaeus, although he certainly developed the system massively by naming so many plants and animals in this way. It was started in the early seventeenth century by the Swiss botanist Johannes Bauhin. Of course, back in those days everyone who was even slightly educated knew Latin anyway, so it is no surprise that scientific names are in this erstwhile international language. Some papers are written giving the common English name only. This is inadequate and often confusing: for example, there are two *chrysanthemum leaf miners* (Section **5.2.2.1(a)**) in different orders! And to contract, say, the chrysanthemum leaf miner to CLM, is even worse. It may save the printer's time but wastes the time of many readers, which is more significant. Irritatingly, larval insects are often popularly called *worms* with which they have an extremely remote ancestry. Unfortunately, this habit is too deeply entrenched to be extirpated, as in the use of *wireworm* for *elaterid larva*. But in some cases all is not lost: therefore *Choristoneura fumiferana* is preferably called the *spruce budmoth* rather than the *spruce budworm*. The name carries more useful information. Then for *armyworm* the French term *chenille legionaire* is much more expressive.

Evolutionary change occurs at four levels: (i) within populations; (ii) between populations, where it may lead to: (iii) speciation; and (iv) macro-evolutionary levels, namely the formation of higher taxa such as genera and families (Wright, 1982a; Maynard Smith and Szathmáry, 1995; see Section **9.10**). New species usually form when populations become reproductively isolated in what was formerly a single species (q.v.). After speciation the two resultant species will still have most of their genes and gene arrangements in common, but in particular differ in genes that prevent interbreeding. Through time, however, they will acquire several more genes that separate them further. The gene pool records the species' history. Even so, because of conservatism in biochemical pathways a majority of genes are common to a wide range of organisms (Section **9.1**). For example, the gene *McIr*, which codes for melanin synthesis in mice, is believed to be similar to one in the melanic variety of the moth *Biston betularia*, and the well-studied shell colour and banding polymorphism in the land gastropods, *Cepaea nemoralis* and *C. hortenis* are almost identical and have a similar genetic basis (Ford, 1975). Indeed, there are a large number of *major genes* that are responsible for universal effects in organisms, plus an even larger number of *minor genes* that code for the remaining variation (Fitzpatrick *et al*., 2005).

Taxonomy is inevitably a continuing study. One of the long-standing problems is species with multiple names. The same species has been described more than once by different taxonomists, generally without either being aware of the fact. When this has happened the name given first takes precedence. In detailed biological research the name of the author, and sometimes even the year of description, are appended to the scientific name, therefore helping to resolve the problem. But *cryptic* and *sibling species* are a nightmare. If in preliminary work two or more species are suspected, but not demonstrated, within an erstwhile good taxonomic one, they are referred to as the former. Then later on, species that have behavioural differences, are *shown not to interbreed in nature*, but even so are morphologically indistinguishable, at least as adults, are referred to as the latter. Undetected sibling species (cryptic ones) are a source of confusion and error in both pure and in applied entomology (Walter, 2003). Thus in the early days, one of the malarial mosquitoes in Europe was called *Anopheles maculipennis*, the spotted-winged anopheles. Today this species is recognized as a *species complex*: *An. maculipennis* sensu lato (= s.l., in the wide sense). *Anopheles maculipennis* sensu stricto (= s.s., in the strict sense) is one of the sibling species comprising this complex, and so are *An. sacharovi, An. labranchiae* and *An. melanoon* (Section **7.3.2.4(d)**). They may be distinguished morphologically, however, by the surface patterns of their eggs. Then, two sub-species of *An. melanoon* have been found. Sub-species require three names, here *An. melanoon melanoon* and *An. melanoon subalpinus*. The sibling species of the *An. gambiae* complex are distinguished by another criterion, the bands on their polytene chromosomes. But what has led to great confusion is that within the *An. gambiae* complex some of the sibling species transmit malaria and others do not (Section **7.3.2.4(d)**). Molecular studies (Williamson, 1992), however, are presently improving taxonomic resolution. But the problem is not confined to mosquitoes; it is far reaching. The biting gnat, *Simulium damnosum* (Section **7.3.2.4(i)**) is similarly complex. Recently, it has been shown that the whitefly, *Bemisia tabaci* (Section **5.3.1.2(c)**), may comprise at least 24 morphologically inseparable species (Xu *et al*., 2010).

1.5 The Function of Insect Stages

It is fundamental that, because insects must shed their dead exoskeleton periodically in order to grow, they *necessarily* develop in a series of stages. Through millions of years of evolution, and remember that insects pre-date the dinosaurs, these stages have been modified for several different biological functions as juveniles develop towards adulthood. This is termed *metamorphosis* (Section **1.4.3**). And as we have seen, these modifications, although notable in aquatic palaeopteroids, are generally more extreme in the Endopterygota.

In the egg stage, embryological development to the nymph or larva takes place. Usually this occurs after oviposition, but in some cases, for example in blow flies, such development to the larva is nearly complete at this time and hatching proceeds quickly. In contrast, in some other groups the egg stage functions to bridge a period of harsh physical environmental conditions, such as drought (plague grasshoppers) or the depths of winter (temperate aphids, winter moths). In those species in which the egg stage spans a period of heat and dryness, the chorion is highly modified to resist desiccation while also allowing respiration to take place. The astoundingly detailed work by Hinton (1981) on this subject is and will remain a classic study.

As we have seen, exopterygote nymphs in terrestrial situations normally function like miniature adults that are flightless and do not reproduce. They often share the same microenvironment with the adults, a feature much less common in endopterygotes (Bryant, 1969), who normally inhabit different *juvenile* and *reproductive* environments. But while the primary function of the larva is to feed, it must also survive and may disperse. These larval functions, in contrast to those of nymphs, are not restrained by the future functions for which adults are selected, because the pupa allows for a total restructuring. Therefore a caterpillar is primarily a walking alimentary system. Just like a miniature cow, its relatively big gut is required to digest large quantities of poor quality food, usually with the assistance of symbiotic microbes (Section **10.2.2.6**). During development the larva elaborates an extensive fat body, an energy and protein store of the building blocks from which to construct the adult. Even so, such larvae, and especially those feeding externally, employ a variety of devices to reduce predation and parasitism (Section **5.2.1.3(b)**), that is, there are also mechanisms for immediate survival.

Coloration provides important survival strategies for exposed larvae (Section **5.2.1.3(b)**). It commonly blends in with that of the food material, reducing the visibility of the larva to its enemies, a device called *cryptic coloration*. A quite different strategy is to sequester poisonous substances from food plants. The larvae doing this often use bright colours to advertise the fact that they are dangerous, a system known as warning or *aposematic coloration*. Endophytic and soil-dwelling larvae, being hidden, are often brownish or depigmented. In exposed larvae, diurnal movement may also assist survival: movement and survival are linked. Cryptic larvae normally feed only at night, therefore avoiding predation from birds, lizards and the attention of most parasitoids. Larvae that attack herbs frequently hide in the litter or soil below the plant during the day. Older caterpillars of *Lymantria* (Section **5.2.1.4(f)**) and the tropical, defoliating moth *Melipotis* move from the canopy of the tree at night to its base during the day, but such cases are unusual for arboreal species. Therefore, when the questing entomologist finds *fresh*, biting damage to plants it is well to search potential refuges for larvae.

Apart from aerial dispersal in the young larvae of some forest moths (Section **5.2.1.4(c)**), local dispersive movement may occur as the larvae age. Caterpillars are sometimes gregarious when young but are later solitary, like those of the white butterfly *Pieris brassicae* and of the sawfly *Nematus ribesii*. Then, mature larvae often disperse briefly. This has two main functions. First, centrifugal movement from the feeding site results in a rapid decrease in *population density*, that is, the number of individuals per unit area (Sections **9.3** and **10.2.1**). This means that they become safer, since enemies have a more time-consuming job searching for them. If several mature larvae occupied a 1 m^2 food plant and then moved up to 5 m from it to pupate, the initial pupal density would be about one-eightieth of the final larval density. This is an example of *density-dependent movement* avoiding *density-dependent mortality* (Section **9.4**). Against this potential gain must be set a possibly greater chance of suffering predation *during* dispersal. Second, larvae seek a hiding place with a favourable microclimate for pupation. Tsetse fly females retain and nurture a single larva in a uterus until it matures, then release it at such a suitable site.

Exposed pupae, such as those of butterflies, are often cryptically coloured too. In some swallowtail butterflies the pupae in a brood may be either green or brown, that is, there is cryptic polymorphism (Sections **1.3.3** and **10.2.3.5**). This has two effects: (i) it allows the mature larva to seek a wider variety of backgrounds on which to pupate, indeed pupal colour normally matches background colour; and (ii) it reduces the effective population density of pupae even further since potential predators treat green and brown individuals as different sorts of prey. Moths usually have pupae concealed within silken cocoons, which the larvae spin with a secretion from their labial glands. Apart from affording some mechanical and physical protection, the cocoon may also provide cryptic protection by incorporating fragments plucked from its immediate microenvironment. In the tropical, solitary mud wasp, *Trypoxylon palliditarse*, late larvae spin a cocoon and then put sand grains into its matrix, therefore constructing a barrier impervious to parasitoids (Section **12.4**).

In the juvenile stages of several pterygote insects, additional specialized stages may occur. Thus in desert locusts the first nymphal instar is worm-like, facilitating its ascent through the sand. The final nymphal instar of mayflies is a *dun*, a stage adapted for escape from its aquatic environment. The first larval instars of several endoparasitic wasps have relatively huge mandibles, weapons providing a final solution to superparasitism. These cases are referred to as *hypermetamorphosis*. Entomologists have never been afraid of long words!

Now we look at the functions of the adult. First, consider a few basic things about its gross anatomy. Adult insects usually show a sharper division into the three body regions (head, thorax and abdomen) than do the juvenile stages, particularly in the endopterygotes. Morphogenesis proceeds in semi-independent compartments (Raff and Kaufman, 1983, in Endler and McLellan, 1988). The head is the *sensory* and *control centre*, but also has the mouthparts, just like a vertebrate. The thorax is the *locomotory centre*. The abdomen is the *visceral* and *reproductive centre*. If one compares a blow fly maggot with a blow fly adult the difference is very clear. The maggot is effectively headless and has no obvious division between thorax and abdomen. The adult has a well-defined head with complex mouthparts and diverse sensory equipment, including huge multifaceted eyes with ~240,000 neurones in the brain to process their information, antennae with thousands of sophisticated sense organs, and so on. It has a thorax packed with flight muscles using oxygen at a rate per unit mass similar to that of hummingbird wing muscles, and an abdomen with a reproductive system that can produce over 500 progeny in a week. The ensemble can deliver these eggs to several suitable larval feeding sites kilometres distant from each other and its natal environment. If we could construct a machine capable of this, one weighing <100 mg (a mini-drone), then we could say fairly that we have reached the technological age.

The broad generality is that adult insects redistribute themselves (disperse or migrate, see below) first and the survivors seek resources and reproduce afterwards. Exceptions are in a small minority. The distance such individuals may travel varies from a few metres to hundreds of kilometres. In the first case, many little Sternorrhyncha, such as psyllid bugs and scale insects, redistribute themselves over several generations within the same tree. But diminutive diamond-back moths (Section **5.2.1.4(a)**), which are not much bigger, may fly up into the clouds and be transported hundreds of kilometres in a few days.

In outbred species the numbers of the two sexes are roughly equal (Fisher, 1930). As Clarke (1984) expressed it humorously: 'The Almighty and Ronald Fisher between them decided that in general the ideal ratio between males and females should be 1:1.' But in inbred situations females predominate. When this occurs, for example, when entire progenies develop in confined spaces, as in *Melittobia* (Section **8.2.2.1**), females bias the sex ratio of their progeny towards daughters (Hamilton, 1967). Furthermore, several insect species are parthenogenetic and in a few males are unknown. The MPF : female ratio varies according to species, from one in some aphids to 10,000 or more in the Australian swift moth *Abantiades* (Section **10.2.5.1**), some tachinid flies and eucharitid wasps.

Many tropical insect species have several generations per year, they are *multivoltine*. This also occurs in several temperate species, such as blow flies. Here different generations are subject to different selective forces, particularly from the physical environment (Moran, 1992a). As one moves poleward an increasing proportion of species become *univoltine*. Even so, in an inclement summer they may not be able to complete development. Nearer the poles many species need more than a year to complete development (Section **10.2.2.2**).

When a patch of food lasts only as long as the period of development, all emerging adults must disperse to find a new one (Section **12.2.4**), so all adults should have similar flight capability. But where this patch lasts much longer, only some of them need to disperse, and we often find that the dispersive capability of these adults is far greater than that of those that stay. There is therefore a *flight polymorphism* (Section **1.4.3**). Consider the adults that disperse. A rough and ready relationship exists between an insect's size and its speed of flight (air speed), namely *all* small insects are slow fliers, and *some* large insects are fast fliers (Fig. 1.3) (Lewis and Taylor, 1967; Brackenbury, 1995), with speeds varying from ~0.5–10.0 m/s. Small insects cannot fly faster than a light breeze, so that they fly either near to the ground where the air speed is low and hence may have some control over the direction of their flight, or they fly up and let the wind carry them where it will. One can see that the spatial scale of these two modes is quite different. The first is termed *dispersal*, the second, namely flight between habitats, is *migration* (Hassell and Southwood, 1978). Small insects that undergo a long, largely passive dispersal high in the air, on finding food, usually move only in a restricted ambit during reproduction. Many aphids and the fruit fly do this. Others, like clover weevils, lose their flight muscles once they have found the breeding site, hence becoming flightless and limited in their area of operations.

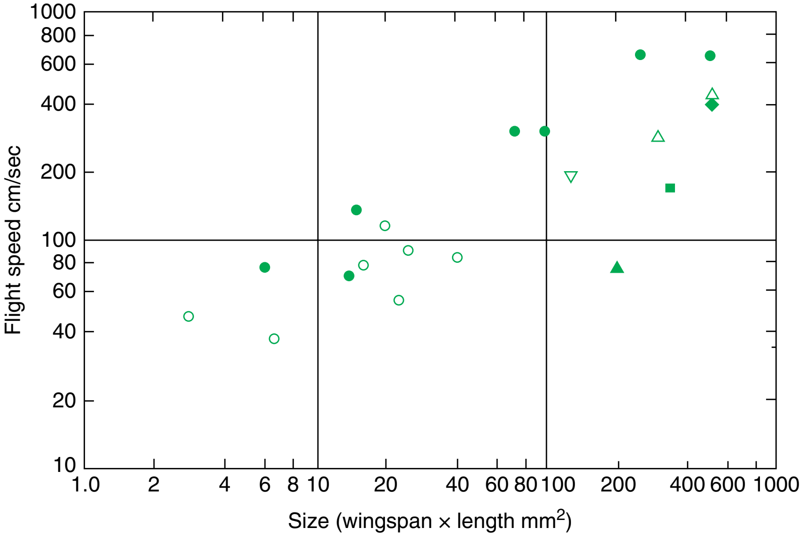

Fig. 1.3. Flight speed and size in insects: all small insects are slow flyers, some large insects are fast flyers. Adapted from Lewis, T. and Taylor, L.R. (1967) *Introduction to Experimental Ecology*. London, UK: Academic Press. Redrawn with permission.

Medium-sized and large insects, especially in the Hymenoptera, Lepidoptera and Diptera, are usually strong fliers and can progress against a moderate breeze if they stay near the ground. By contrast, beetles are not normally strong flyers and also lack ocelli (Kalmus, 1945). Selection has promoted protection not speed. Honeybees, noctuid moths, big pierid butterflies and tabanid flies can fly up to ~5 m/s (18 km/h) in still air. They have a high *individual searching capability* (ISC) and never lose this capacity during reproduction (Section **10.2.4.1**). Maximum speeds >10 m/s (36 km/h) are known for aeshnid dragonflies and hawk moths (Dudley, 2000), about the same speed as the world's fastest sprinter.

Related to capability, they deposit their eggs in several widely separated places. Placing eggs in several patches means that the female literally 'does not put all the eggs in one basket'. A catastrophe befalling one egg batch will not kill all the eggs. This strategy is termed '*risk spreading*' and we refer to it again in Section **9.7**. In effect, the female reduces the overall population density of the progeny on a scale related to her ISC. Recall that while the dispersal of larvae about to pupate has a similar ecological effect, they reduce their *own* population density (Sections **9.2** and **9.3**). An odd case of reducing population density of progeny is found in dung beetles. Females roll their dung balls some distance from their steamy site of origin. Population density often has outcomes for the reproductive success of individuals and, as a consequence, for their populations (Sections **9.4** and **10.1**).

At the other end of the spectrum there are insects with very reduced mobility, such as scale insects, that have been termed 'plant parasites'. They lead an analogous life to, say, ectoparasitic lice on a mammal in that the insects spend their entire life on a single plant, living at its expense. But the obvious difference is that their 'host' is not an animal. The comparisons that have been made regarding their ecology (Price, P.W., 1997) are compelling, but they are the more so *because* one group attacks animals and the other attacks plants. Of course, these trophic levels are not the same (Eggleton and Belshaw, 1992). Rettenmeyer (1970) and Turner (1987) make a rather similar distinction when defining mimicry (Section **10.2.3.5**), excluding cases, under the heading of *protective coloration,* where insects resemble plant parts or inanimate objects, for example, katydids resembling leaves and moths resembling faeces. Where insect herbivores become closely associated with their plant food (Price's 'plant parasites'), as in many homopteroids, this leads to speciation and adaptive radiation with several parallels to ectoparasites. But some plants such as dodder (*Cuscuta*, Convolvulaceae) and mistletoe (*Viscum*, Loranthaceae) live on and at the expense of other plants, and so are genuine plant parasites. Also coming to mind are protists such as *Phytomonas* (Camargo, 1999). These have no connection to bugs such as scale insects. Therefore it is better not to attenuate the term 'parasite' and to separate it from 'parasitoid' and 'micropredator' (Section **7.1** and q.v.). Nor do I use the term 'host plant'; here they are called 'food plants' as they always used to be. The fact that plants provide facilities to insects other than food is covered in the term 'resource patch' (q.v.). As J.S. Kennedy (1953, in Dethier, 1954) puts it, a food plant 'is not merely something to be fed on, it is something to be lived on'. Neither do I regard carabid beetles as occasional 'seed predators' (the *Short Oxford English Dictionary* (SOED) defines prey as 'An *animal* that is hunted or killed'). We know all these organisms transfer energy between the trophic levels and may share common *biofacies* and co-evolutionary features.

Then there are practicalities. In describing biological interactions between a pest insect, its food plant and its parasitoids (*tritrophic interactions*), the generic use of the term 'host' makes for difficult reading and can lead to ambiguity. For example, in a paper by Preszler and Price (1988) entitled 'Host quality and sawfly populations: a new approach to life table analysis', is the host the sawfly or its food plant? Again, Kirk (1991) uses 'host' to refer to both plants and animals. While the SOED also defines this word generally, I think that in biology its use should be restricted to animals, otherwise the end point is to have sheep viciously 'predating' pastures! Some biologists would not agree with me, but see Hawkins *et al.* (1990) and Speight *et al.* (1999, p. 88), who do.

1.6 Insects as Vectors and Pollinators

Insects, being mobile and a handy size, are frequently employed by less mobile organisms to seek and find new requisites. Pathogenic microbes exploit them to find new hosts; flowering plants do so to distribute pollen (male gametes). While microbes, unless symbiotic, do not reward insects for their services, flowering plants usually do (Section **8.2.1.1**). The best that microbes usually do is to interfere minimally with an insect's ability to seek and find requisites, thereby furthering their own imperatives (McNeill, 1976). But *symbiotic* microbes may improve growth and defend insects in various ways (Section **10.2.2.6**). And with phytoplasmas (Section **5.3**) there is evidence that infection can improve the vector's reproductive success. All of these are probably co-evolved situations.

Pathogenic microbes infest both plants and animals, but there is little overlap in the taxa attacking these kingdoms. Two orders possessing piercing and sucking mouthparts, the Hemiptera (Exopterygota) for plants and the Diptera (Endopterygota) for animals, are the most important vectors. In Section **1.2** we distinguished *biting* from *sucking* insects, and *exopterygote* from *endopterygote* insects: therefore basic taxonomy has consequences for pathology. Plants are immobile while most animals move actively: it may be no coincidence that Hemiptera are the major vectors of plant pathogens, while the more agile Diptera commonly transmit pathogens that attack tetrapods. But this is conjecture (Section **11.5.1**).

1.7 A Note for Students of Pest Insects

Chapters 3 to 7 contain examples of pest insects selected for their importance and/or their interest, giving an idea of their global range, contrasting their ecologies and economic importance, and providing a starting point for research. The list is far from exhaustive. Even so, most of the pests have to be dealt with briefly. Much more is known about all of these insects than can be given here. But so that one can begin to appreciate the *depth* as well as *breadth* of knowledge, certain pest species have been highlighted. These were selected because: (i) I have personal field knowledge of them; (ii) they are economically important; and (iii) taken together they illustrate a contrasted range of ecologies and are used as examples in the ecological chapters (Chapters 9 to 12). At the other end of the scale, a few less important but related pests may be named at the bottom of the section on a main pest. Hence, we deal with pests on three levels of detail: highlighted, basic and additional. More comprehensive lists appear in Hill (1997) for world pests and in Pedigo (2002) for North American pests. The pests of vegetables are covered in McKinlay (1992).

Two general points remain. The spatial scale on which a pest operates depends both on its numbers and on its redistributive capability. For medical and veterinary pests, area-wide control is an ideal. Plant pests operate on a variety of scales. Locusts and aphids, for example, operate on vast scales, as billions of individuals can migrate hundreds of kilometres. Colorado beetles and gypsy moths operate on a scale of only a few kilometres. But the scales on which we deal with plant pests are essentially horticultural and agricultural ones. Horticulture means 'culture in gardens' (Latin: hortus – a garden), while agriculture means 'culture in fields' (Latin: ager – a field). In the former we deal with a confined space, the garden, in which each plant can get individual attention from the gardener. The word 'orchard' comes from the Old English 'ortgeard', and the 'ort' bit probably comes from 'hortus'. In agriculture, we deal with spaces measured in tens of hectares, so mass methods must be employed. The culture of vegetables was largely within the province of horticulture, but over the past decades more and more of them have been grown on an agricultural scale. This yields a cheaper product, albeit with for various reasons some reduction of quality, as you may have noted!

2 An Introduction to Plant Pests

2.1 Classifying the Material

Before starting to classify our pests, we look briefly at classification in general to provide some insights. While hypothesis generation and testing are familiar (Popper, 1989; McShea, 1998; Stephens *et al*., 2006), the role of classification and comparison must not be marginalized (Maynard Smith, 1983b; Rieppel, 2004). Put simply, a series of observations is made. In biology these often derive from natural history (Applegate, 1999). Then, after selecting what is useful (Maelzer, 1965), like is put with like into a set of conceptual slots in order to compare them. Aristotle divided the four known elements into those showing gravity (earth, water) and those showing levity (air, fire). When chemistry had developed, and many modern elements had been recognized, Mendeleev (1869) formed the Periodic Table by placing those with similar chemical properties together. Only when this had been done could it be found that these properties changed systematically according to the atomic weight of each element. Without such a conceptual framework this finding would have been impossible.

As a simple example, imagine collecting a bag full of stones from a fast-flowing section of a stream. Throwing them out on a bench they appear as a jumble of sizes and colours. But if we *classify* them by size and colour we may find that these properties are related: the white ones (limestone) are generally smaller than the black ones (flint). Then we may *hypothesize* that limestone is softer than flint and so wears down faster in the current. Without labouring the point, we see easily how such examples can lead to further hypotheses.

Then in parametric statistics, numerical data may be analysed initially by constructing a frequency histogram (Bailey, 1994). Once the data are so ordered, the type of statistical distribution they present can be found, leading to appropriate forms of further analysis and hypothesis generation. Non-parametric data can be ordered in a contingency table. In early biology, both Linnaeus and Buffon produced taxonomic classifications, that of the former providing a start to modern classification. Hypotheses were not being tested: advances in understanding were made simply by placing like with like. Any points of argument concern the classificatory criteria that best improve understanding, ones relative to the circumstances.

T.H. Huxley outlined the function of classification as 'to facilitate the operation of the mind in clearly conceiving and retaining in the memory the characters of the objects in question', while Herbert Spencer, following Francis Bacon (Fig. 2.1), said simply: 'Science is organised knowledge'. Classification is the recognition of pattern (MacArthur, 1972; Lawton, 1996), which may lead to explanatory, predictive, testable and potentially refutable hypotheses. It always has purpose (Rieppel, 2004). An example is Endler and McLennan's (1988) heuristic classification of the evolutionary process (see their Table 1); it extends knowledge and identifies gaps within it. Finding gaps promotes advances. While classification and comparison are no substitute for experimentation (Antonovics, 1987), they are a path towards it (Bradshaw, 1987; Vet and Dicke, 1992). Hypotheses can be modified as data accrue. Statistics often provides a rigorous and necessary comparison (Stephens *et al*., 2006). Also, much biological order derives from the evolutionary process itself (Kauffman, 1993; Price, P.W., 1997; Rieppel, 2004). Indeed, natural taxonomy is essential for the progress of biology (Sokal, 1985; Walter, 2003). The World Biological is greatly diverse, it has 'appalling complexity' (Thompson, 1939) and requires formal classification to seek pattern and generality. But our predilection to generalize is frustrated by this complexity (Hassell and Southwood, 1978). And as Elton and Miller (1954) caution: 'It is possible to destroy any classification by introducing transitional or exceptional categories in sufficient numbers.' The Devil is in the detail.

Fig. 2.1. Francis Bacon, the promoter of empiricism at the start of the Enlightenment. Source: Wikimedia Commons.

Other useful generalities exist. In several areas of biology, especially in ecology, *space and time may be comparable and complementary dimensions*. There are temporal and spatial patterns (Spencer, 1864; den Boer, 1968; Freeman, 1976; Levin, 1992; Brown, J.H. *et al.*, 1995). We can compare *time-dependent* processes with those that relate to space, and may be *time independent*. For example, den Boer (1968) noted that organisms could spread risk from *inimical factors* (q.v.) in time as well as in space (Section **9.7**). Habitats and patches (Section **12.2**) have spatial extent and duration (Southwood, 1977; Holling, 1992). There can be *enemy-free space* and *enemy-free time*, both diurnal and seasonal (Andrewartha and Birch, 1954), and spatial limitation and temporal limitation. Refuges (Section **9.9**) may be spatial or temporal. The regulation of insect stages during the year (*phenology*) and their adjustment to the seasonal distribution of resources (Section **9.8**) may be integrated conceptually with their search for these same resources in space. Individuals should be in the right place at the right time to maximize their reproductive success. Hence, if we are considering a time-dependent process in biology, it is always useful to enquire if there may be a space-dependent equivalent (Freeman, 1976).

Time-dependent processes in ecology refer basically to a sequence of actions: one thing follows another in a causal chain. The 'Angelic Doctor', Thomas Aquinas, in about 1260 used such a chain as proof of the existence of God, the final cause for the observable existence of the Universe (Russell, 1961). For us, changes in the physical environment often have biotic effects on several temporal or spatio-temporal scales (Levin, 1992), with these effects also having sequence. Thus, *in the short term* a sequence of several cues in space and time allow enemies to find their victims (Vinson, 1984) and males or females to find their mates, a catenary behavioural process. A sequence also occurs when an attack by a primary pest makes the plant more susceptible to a secondary attack (Ohgushi, 2005). For example, conifers defoliated by caterpillars are less able to resist bark beetles (Sections **1.2** and **4.2**). For mammalian hosts, primary flies causing 'strike' of sheep may be succeeded by secondary and even tertiary flies (Section **7.4.2.1**). In the infestation of stored products there are primary and secondary pests, while in forensic entomology (Section **8.3.1**) there is a *long temporal succession* of insects invading a human corpse, providing a means of estimating the time of death. Longer successions occur in plant communities passing from associations of initial colonists to those of the climax sere.

Again, for both plants and insects there are space-dependent equivalents. If we take a wide-scale transect, say from the Arctic coast of Russia to the Black Sea, we find that the species succeed each other in a definite pattern. On this scale community ecologists recognize two types of biodiversity. Diversity within communities is termed α-*diversity* while the rate of change of diversity along a long transect is β-*diversity*. Alpha diversity relates the number of individuals (N) to the number of species (S) in the sample and there are several ways to associate these measures (Pielou, 1975; Magurran, 2004). Beta diversity can be calculated by assessing the probability that two randomly selected individuals are conspecific, changes with distance (Condit *et al*., 2002). For an update on such measures, see Barwell *et al*. (2015). Spatial gradients in the physical environment, especially temperature and moisture, also exist and may drive β-diversity. Indeed, physical factors in autecology follow a spatial scale, from global drivers to those in the immediate proximity of individuals (Section **10.1.1**). There are unifying parallels between time and space: both are continuous but exist on several different scales. *Scale*, a further generality (Levin, 1992), being expressed not only in time (seconds, days, years) and space (item, patch, habitat, landscape, region; Section **12.2.1**), but also in *pattern* (Lawton, 1996). While *predictability* is at root a temporal component of environment, there may well be subsequent spatial aspects. But there is a further generality arising from scale: large objects whether living or inanimate tend to have longer duration than small ones (see Sections **10.1**, **10.1.1**, **12.2.1**)

Another general environmental feature is order versus chaos (Ellner and Turchin, 1995). This is illustrated by the causes of change in global weather patterns. The main and *predictable* driver is the dynamic relationship between the Earth and Sun (Section **2.2.2**). In winter in higher latitudes we know that day length is always shorter and weather usually colder than in summer. A small-scale pattern 'is imposed by a larger scale constraint' (Levin, 1992). But the interplay of factors such as atmospheric pressure, precipitation and evaporation (water vapour is a major greenhouse gas; Barry and Chorley, 1995) causes terrestrial environments to become increasingly complex and *unpredictable*. Witness the success rate of weather forecasts. For organisms this naturally relates to den Boer's *risk spreading* (Section **9.7**), that is, their evolutionary response to *unpredictable* events. But the richness of such interactions ostensibly allows complex systems to undergo *spontaneous self-organization*, producing order in the midst of chaos (Prigogine, 1980; Rind 1999; Section **9.8** and see also **11.3** for a precise definition of chaos).

A further useful duality, when parameters are being estimated in ecological data, is the relationship of the variance to the mean. For example, the relationship of the $\log_{10}$ variance to the $\log_{10}$ mean numbers describes the tendency of populations to aggregate (Taylor, 1961), while the *variance* of the sex ratio between broods in the Parasitica (Section **8.2.2.5(j)**) gives new insights into their reproductive strategies (Hardy, 1992).

Here we use classification in several ways to organize material. We arrange insects by taxon, order the plants and animals they attack, organize the biological and numerical aspects of insect ecology and classify the various insecticides that farmers use. But just as in language where one can say the same thing in several ways, there is often more than one way that biological material may be classified (Lawton, 1996) and there is more than one way in which plant pests could be ordered. One could use the ordinary taxonomic system: go through the insect classification from Protura to Strepsiptera discussing representative pest species. This has little to recommend it for economic entomology unless one is using the book simply as a reference to pest species; but there is an index for that. If, on the other hand, one is learning the subject and has just made a first stab at insect classification, it is likely to induce narcolepsy. And interest is the key to learning. Even so, there are many instances in which comparisons within and between taxa improve our understanding of insect ecology and behaviour (Varley, 1941; Jayasingh and Freeman, 1980; Freeman, 1982; Price *et al*., 2005; Richards *et al*., 2009).

One could also use the type of crop for classification. This is fine if one is concerned with specific crops, but the question arises of how one would classify them. One could, of course, use the scientific plant classification, or what is more helpful to the agronomist, classify them by their products. We could distinguish grain crops, fodder crops, root crops, fruit crops, and so on. But this classification is hybrid. There is an element of plant taxonomy in it because, for example, nearly all grain crops (excepting amaranth, Amaranthaceae) belong to the grass family Gramineae, but some grasses, along with several brassicas and legumes, are grown for fodder. Then it has an ecological component because both grain and fodder are field crops.

Finally, there is the ecological classification used here. It is based on a system I developed long ago when teaching applied entomology in the University of London. Using that part of the plant's anatomy that the pest normally attacks, which is a component of the pest's immediate environment, one can make insightful comparisons across different ecological and economic situations, crops and insect groups. Given insect species tend to consume specific plant parts (Root, 1973; Ohgushi, 2008), one can compare different pests within the same microenvironment, that is, 'What common problems do root pests share in locating their food?' and, following this, 'Is there a common approach to their economic control?' Also, juvenile insects attacking different plant parts have different patterns of mortality (Price, 1984; Cornell and Hawkins, 1995). Similar systems are often used in economic entomology (Long and Hensley, 1972; Kisimoto, 1984).

But of course, even the insects that attack the same plant systems do not have *identical* ecology. Although there are commonalities that would be missed without making comparisons, the plants they attack may be very different in growth form, longevity and physiology. Then there are big differences between the various taxonomic groups of the pests themselves. As we saw above, piercing Hemiptera and munching caterpillars in the same situation cause a different type of damage. Larval beetles often develop more slowly than larval flies do. Again, taxonomic associations occur within this ecological classification. For example, the Hemiptera comprise most of the sucking feeders while Coleoptera form a majority of the borers in woody stems. Finally, there are different ways that the insect species utilize the same plant part: leaves can be eaten from the outside or inside, even rolled up to provide a refuge.

Wider spatial scales of comparison must be considered too. First, there are many distinctions between forest and field. Forest pests usually occupy large areas and the damage they cause is often high above the ground, making monitoring difficult. Forest trees are long-term crops and crop rotation as a means of control is debarred. With field crops the converse is true: access and inspection are simple and the crops short term. Pests of forests are almost never pests of field crops, giving further classificatory value. Orchards and vineyards are to an extent intermediate. Second, a distinction exists between geographical regions. Although many pest insects are cosmopolitan or migrate from warmer to cooler temperate zones in spring, division of our pest species by global regions is limited and we can often see that their ecology changes relative to these zones. Thus aphids often reproduce both sexually and asexually in cold climes but only asexually in warm ones. An ecological classification enables one to make revealing comparisons between tropical, Mediterranean and temperate environments and between the agro-ecosystems of these contrasted areas. The crop-type approach would not allow global comparisons to be made so well, as the main tropical crops are not grown in temperate regions, and often vice versa (maize, onions and carrots are some exceptions). Related to this, we have transported crops more on an east–west axis than on a north–south one (Diamond, 1999).

An ecological approach gives us a fuller insight into pest operations and how their economic control may be achieved, particularly as we are now endeavouring to eliminate insurance spraying. Since each pest species has its unique ecology it helps us find the weakest link. For example, underground pests usually have difficulty in moving through hard soil. Soil compaction with a heavy roller is thus a cultural means by which we can reduce their movement and hence the damage they cause. I will often refer to weakest links in a pest's life cycle and show how they may lead us to efficient means of economic control. While the specifics of control change with time, the ecology of pests is less changeable. We note, however, the important principle that *insect species always show evolutionary adaptation to environmental changes*, including those we induce.

Another point, rarely made, is that the taxonomic groups from which crop plants have been developed are not a random collection from the plant kingdom. Crops are mainly the cultivated varieties (= *cultivars*) of the flowering plants or Angiosperms. But within this dominant group only a few families contain several crop species. For example, we have the Cruciferae (brassicas, turnips), Rosaceae (top fruits such as apples, pears, plums and cherries, and strawberries), Papilionaceae (peas, beans and lentils, and fodder crops like clover and lucerne), Umbelliferae (carrots, parsnips, parsley), Rutaceae (citrus), Malvaceae (cotton, okra), Cucurbitaceae (cucumbers, pumpkins, melons and courgettes), Solanaceae (potatoes, tomatoes, capsicum peppers and aubergines), Vitaceae (grapes), Gramineae (all cereals, sugar cane), Musaceae (bananas) and Chenopodiaceae (sugar beet). Many of these groups are ruderal annuals. We have noted only 12 of approximately 250 plant families here and these contain the great majority of the world's crops. Furthermore, in terms of crop weight a dozen species comprise 80% of the world's tonnage: wheat, maize, barley, rice, sorghum, sugar cane, potatoes, sweet potatoes, cassava, soya beans, sugar beet and bananas (Diamond, 1999).

In non-flowering seed plants or Gymnosperms, many coniferous trees are used to produce wood and paper, or are planted as ornamentals. Sago comes from the various palms, including some primitive cycads. Then, a few fungi, such as truffles and mushrooms, yield products of commercial value. All of the plants have insect pests. While some seaweeds are eaten in several parts of the world, insects, being a very minor element in the marine environment, do not attack them.

2.2 Physical Drivers and the Global Distribution of Plant Associations

2.2.1 General introduction

We will deal with insect pests from three climatic regions: tropical, Mediterranean and temperate. People increasingly move around the world, consequently wherever students start and wherever they end up, they should have a global view of ecology in relation to economic entomology, a knowledge that helps to foster international dialogue. And as we have seen, the comparative approach is a powerful aid to understanding.

When early Europeans grew crops and built dwellings they cut down, burnt or drained much of the virgin woodland or marshland. They used a considerable amount of timber for dwellings, and straw and marsh grass (*Phragmites*) for thatch, both of which are carbon sinks. Since their populations were small, cultivated fields were limited areas wrested out of large expanses of the original plant community, largely broad leaf forest. Such was the scale of this process that by 1000 AD not a single undisturbed forest existed outside Fennoscandia. For example, instead of being cleared islands for crops and grazing within the forest, the fields coalesced and the forests became islands in the fields. Diversity, however, was increased rather than reduced. The pests we endure now are often derived from these original communities, although some are imports from more distant places. Most did not feed originally on the forest trees but on the herbaceous plants present in regenerating areas following fire, landslide or the fall of a great old tree. But where agriculture is fully developed the situation is now quite different and outside urban areas cultivated crops comprise the majority of the land area. In all, between 1700 and 1980, 12 million km^2 of forest has been converted into croplands (Pearce *et al.*, 2007). Now, and for various reasons, the pests may come from farther afield. Where human populations are dense the existing natural plant communities are delineated largely by our activity, they are reserves protected to a greater or lesser extent from the depredations of thoughtless people or of those with avarice in mind.

On a different tack, it is well for the economic entomologist to understand the basics of climate that comprise the physical aspects of ecology and the main factors that determine the global distribution of the major plant associations. In the early days the crops that were grown were mainly derived from cultivars of wild species originating in the same regions. In the Anatolian region of Turkey some 8000 years ago, native wheats were fed to livestock; only later were they eaten directly by humans. The Indigenous Peoples of South and Central America have been cultivating various local Cucurbitaceae for as long as 11,000 years (Jones, 1999). Since then, desirable crops have been introduced into most parts of the world where they can be grown (Diamond, 1999).

2.2.2 Physical determinants of vegetational distribution

2.2.2.1 The global picture

Since we consider insect ecology from all global regions and follow the spirit of Robert MacArthur (1972), we now examine the drivers of the Earth's climate and the gross distribution of its vegetation upon which insects primarily depend. In about 1800, after extensive travels in the Caribbean and South America, Baron Friedrich von Humboldt suggested the existence of *vegetational zones* and their relationship to latitude and altitude. His ideas were extended in 1855 by Alphonse de Candolle who argued that these zones were set by climatic imperatives, especially temperature and moisture. Today we recognize that the type of plant association is determined by two primary factors (latitude and precipitation) and three subsidiary factors (topography, the proximity of the sea [invariant landscape factors] and soil type [edaphic factor, also effectively invariant]). Mean annual temperature depends primarily on latitude, but also on several other influences, especially altitude and the global advection of air and water masses. Temperature is the main driver of climate but is influenced by other physical factors. Temperature and precipitation, mainly rainfall, are the *proximate factors* controlling vegetational distribution on land (Whittaker *et al.*, 1975; Colinvaux, 1986; Polis, 1999), but subtle interactions occur between both of them (Fig. 2.2). Fundamentally, the climates of each latitudinal zone, whether they are cool or hot, wet or dry, depend on the dynamic relationship between the rotating Earth and the Sun. Wellington (1954) says: 'It has never been very sound policy to ignore the possible effects of solar phenomena on meteorological events, although it has often been a popular pastime.' But we now understand that while the solar forcing of the global climate is primary, feedbacks within the system may be even larger (Haigh, 2001; Rind, 2002). Cyclic solar radiation affects firstly the stratospheric ozone layer, with amplifying effects continuing downwards, and then the Equator-to-pole energy transport (Shindell *et al.*, 1999). The interplay of air and water masses near the Earth's surface amplifies the effects of variation in solar energy output (Bond *et al.*, 2001).

The Earth rotates on its axis of presently 23.3° to its orbit around the Sun, its *axial tilt*, in 24 hours giving day and night. It orbits the Sun in 365¼ days giving one year. Time in ecology is primarily *diurnal* or *annual*. The Earth's slightly elliptical path has a maximum distance from the Sun of presently 152 million km on 4 July (*aphelion*) and a minimum of 147 million km on 3 January (*perihelion*). Since the 23.3° angle is maintained during each orbit, the Northern Hemisphere gets more radiation than the Southern Hemisphere from March to September and less from September to March, northern and southern seasons being reversed. Both hemispheres receive equal *insolation* (*in*coming *sol*ar radi*ation*). Near the Equator the period of daylight varies little from 12 hours, but polewards this variation increases progressively in a predictable seasonal pattern.

As well as these familiar basics, there are *short-, medium- and long-term cycles* that affect the Earth's global climate. There is an 11-year cycle in sunspot numbers, first described by Köppen (1873) as a driver of locust plagues. This cycle is caused by variation in deep flows within the Sun's mass. When sunspots are numerous, solar radiation is more intense and the increased heat on Earth is stored temporally in great water masses (White *et al.*, 1997). While the cycles are pretty regular, their amplitude can vary appreciably. Thus, from 1645 to 1715, a period called the Maunder Minimum, peak sunspot numbers were low and

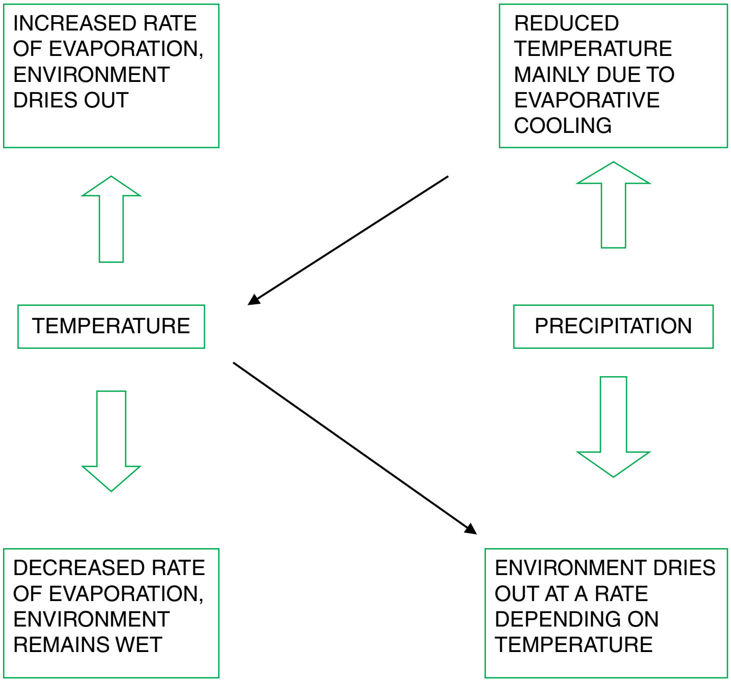

Fig. 2.2. A scheme of relations between environmental temperature and precipitation.

corresponded to a time of reduced global temperatures (Fig. 2.3; Barry and Chorley, 1995; Haigh, 2001). In London, the River Thames froze regularly in winter and fairs were held on the ice. Other such minima (Wolfe, Spörer, Dalton) are known (Bond *et al.*, 2001). Then in the period 1870 to 1915, the summers were cool in central England (Turner, J.R.G. *et al.*, 1987). Cyclonic activity in North America has been related to sunspot cycles (Wellington, 1954). Possibly related to such phenomena or to solar magnetism, 22-year cycles have been found in glacial lake deposits some 15,000 years old (Klvana *et al.*, 2004). A long period of low temperature, the 'Little Ice Age', probably caused partly by cumulative emissions of volcanic eruptions blotting out the Sun, occurred from 1500 to 1850 (Rind, 2002), possibly confounding recent global warming. Crowley (2000) describes changes in the climate of the Northern Hemisphere over the last 1000 years, emphasizing the recent effect of anthropogenic CO_2. Volcanic activity releases huge quantities of dust and CO_2 into the atmosphere, the first resulting in global cooling and the second in global warming. The dust gradually settles and terrestrial plants and phytoplankton remove CO_2, largely as cellulose. Indeed, higher CO_2 levels

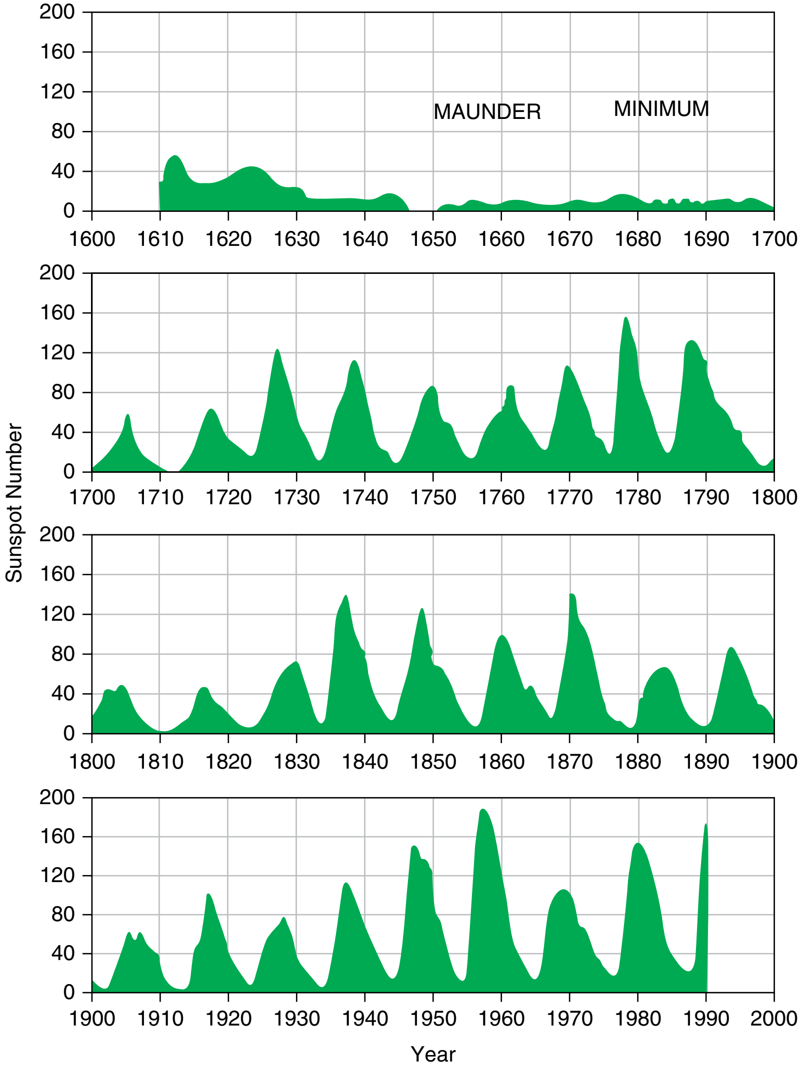

Fig. 2.3. Cycling in the yearly numbers of sunspots from the time of the Maunder Minimum. Adapted from Barry and Chorley (1992) *Atmosphere, Weather and Climate*, 6th edn. London, UK: Routledge.

promote increased plant metabolism if temperature, water (Lovett, 2002) and soil nutrients (Bazzaz, 1990) are not limiting. This applies to both C_3 and C_4 plants (q.v., Wand *et al*., 1999; Denison *et al*., 2003; De Souza *et al*., 2008). Dead plankton sinks and the carbon it contains becomes locked up in oceanic sediments, mainly on the vast abyssal plain which covers ~60% of the Earth's surface. Peat is a terrestrial equivalent and coal is, of course, a fossil carbon deposit.

Such climatic changes concern the ~10,000-year period back to the last Ice Age, the Würm Glaciation. Even within this period there was great variation. In Britain some stadials were of Arctic severity, others were similar to present-day conditions (Coope, 1979). Naturally, glaciations are associated with changes in sea level and hence land area. Then at a frequency of ~7000 years there have been Heinrich Events, of which six are known from 14,000–70,000 years ago. Their existence is deduced from analysis of deep oceanic deposits of limestone carried in icebergs. These events may relate to periods of global warming or alternatively represent an internal cycling within the North Atlantic ice sheet (Hulbe *et al*., 2004). But Heinrich Events correlate with climatic cycles elsewhere, such as dry periods in the eastern Mediterranean.

There are three long-term effects called *orbital forcing variables*, or *Milankovitch Cycles* after Milutin Milankovitch who described them in 1941. The first is due to *precession:* the Earth can be likened to a massive top slowly spinning and slightly wobbling about its own axis. The wobble, which has a mean period of ~21,000 years, results in the apparent changes in the position of the Pole Star and for complex reasons a global variation in the intensity of winter and summer. The second is due to changes in the axial tilt or obliquity between 21.5° and 24.5°. The cyclic change in this angle, which is stabilized by lunar gravitational influence, has a period of ~41,000 years and as a consequence defines a change in width of the tropical zone. With less axial tilt, solar radiation is more evenly distributed between summer and winter, and the difference in receipt of radiation between equatorial and polar regions is increased. Finally, the *eccentricity* of the Earth's elliptical, annual orbit around the Sun varies, having a period of ~100,000 years (Hewitt, 2000). At present, this variation in orbit has only ~7% effect on the Earth's total annual energy receipt, but at maximum eccentricity would cause a 20–30% variation. The interplay of precession and eccentricity, affecting the receipt of solar radiation, has been the main driver of the Ice Ages over the last 600,000 years (Weertman, 1976). The Earth had been gradually warming until about 100 million years ago (Ma), the Coromant–Turnier Boundary, but then may have cooled irregularly, certainly so since the mid Miocene 14.5 Ma (Colwell *et al*., 2008) and culminating in the several Ice Ages over the last 2.4 Ma. The permafrost extended to the north of Spain 20,000 years ago, although mean temperatures in tropical lowlands were only 5°C less than at present.

Continental drift, altering oceanic currents, and mountain building redirecting atmospheric circulation, also have very long-term effects. Then, over the last 500,000 years, data from vein calcite deposits in Nevada (Winograd *et al*., 1992) and ice core data from the Tibetan Plateau and from Vostok in Antarctica, suggest that climatic cycles are not so regular as to have been driven only by Milankovitch phenomena (Rind, 2002). Similarly, data from the rings of ancient Chilean *Fitzroyia* trees going back ~3600 years (Lara and Villalba, 1993) show that on this more limited time scale, temperature variation has been irregular and presents no evidence for recent global warming! Their data also reveal that mean summer temperatures may have an annual variation of as much as 5°C. This variation is associated with cool, wet periods and warm, dry periods in which fires are more frequent in drier forested regions. Such fires leave permanent burning scars on ancient trees such as sequoias (Swetnam, 1993). Over the past few decades, however, while most of the Arctic and northern continents have become up to 2°C warmer, with retreating glaciers and melting ice sheets, Antarctica is about 1°C cooler. This difference may relate to the global distribution of anthropogenic CO_2 emissions. For example, the McMurdo Dry Valleys had lower mean temperatures from 1990 to 2000 (Parmesan, 2006). Cool spots also exist in south-west Greenland and to the north of Hawaii (Rind, 1999), who emphasizes that the global climate is a composite of ordered and chaotic components. Changes are also apparent in tropical forests (Colwell *et al*., 2008). But to unravel the action of increasing anthropogenic greenhouse gases and deforestation, the natural, long-term drivers of the global climate must be fully understood. When other causes of natural climatic variation have been factored out, however, increased greenhouse gas emissions are probably responsible for ~75% of the warming in the Northern Hemisphere (Crowley, 2000).

This constant state of flux on diverse time scales produces dynamic effects in the ecology of plant communities (Grimm *et al*., 1993; Colwell *et al*., 2008) and the insects and other animals that live in them. Climatic periodicity causes periodicity in living organisms (Turner, J.R.G. *et al*., 1987; Koenig, 2002). But each extant species must have retained a pool of genetic variation (Hamilton, 1996) sufficient to allow survival during the relatively rapid and the longer-term changes in their physical environment, although they have often changed their distribution (Coope, 1977, 1979). In geological time, climate has not been a simple extension of the present one and rare catastrophes have had an important role (Ager, 1993). For example, as the last Ice Age subsided, massive floods tore along the valleys from huge released glacial lakes. One such example is the draining of the Laurentide Lakes into the Labrador Sea 8200 years ago, causing the mean temperature to drop by 4–8°C (Barber *et al*., 1999). Another such massive event may have formed the English Channel, although this is disputed.

Getting back to the present, the quantity of the Sun's energy that falls on a unit area of the Earth's approximately spherical surface is determined by latitude, being greatest at the Equator and least at the poles. For our purposes this energy is in the form of radiant light and heat, but due to the Sun's high surface temperature (~6250°C) almost all of it is <4 μm in wavelength: 8% ultraviolet, 39% visible and 53% near infrared. The wavelength of radiant energy is inversely proportional to the temperature of the emitting body, the Stefan–Boltzmann Law. If a beam of solar energy hits the Earth at a right angle, namely when the Sun is directly overhead, as it may be at various times within the tropics, it is distributed over a small area (your shadow is small). But if this beam hits the Earth at an acute angle, as in higher latitudes, it is spread over a larger area, one proportional to the acuteness of that angle (your shadow is large). A larger area receives potentially the same amount of energy and will therefore be cooler and less illuminated because the beam, coming at an angle, has to travel farther through the Earth's atmospheric shell. Therefore, there will be a greater absorption of both heat and light, particularly when aerosols (small salt or dust particles) and water vapour are abundant. The area will be cooler and dimmer than expected. Although day length in summer at higher latitudes is longer than in the tropics, total radiant energy received is less. At Casablanca (33°N), 6.0×10^8 cal/m^2/yr reach the Earth's surface, while at Nottingham (53°N) only 2.5×10^8 cal/m^2/yr do so. Annually, the Low Arctic accumulates only ~600 day degrees above 0°C, the North Temperate ~2500 and the Seasonal Tropics ~10,000 (Danks, 2007), despite the fact that every point on the Earth's surface receives the same amount of daylight (half a year). Plant productivity, which is measured quite well by litter fall, follows this trend. Litter fall in tropical forests is approximately ten times that in Arctic/alpine ones (Bray and Gorham, 1964).

While light and heat input from the Sun have similar general features on arrival, they share a different fate and affect organisms diversely. Light may be absorbed or reflected back into space, partly as radiant heat. Much insolation (also called irradiance) that is lost is due to the reflectivity (*albedo*) of clouds and fallen snow; indeed, the high albedo of the polar ice caps (80–90%) is a contributary reason for their extreme coldness. When snow settles in any area the air temperatures will drop because of the increased albedo, a *positive feedback* system. But soil temperatures will not fall so much because snow is a good insulator. In contrast, in areas with vegetation only some 10–20% of solar radiation is reflected. The albedo of water is highly variable and depends on the angle of incidence of the solar beam. That is why water can appear like a mirror when viewed at an acute angle. Additionally, the atmosphere may scatter light and/or absorb certain wavelengths selectively. In all only ~50% of the Sun's radiant energy reaches land or ocean surfaces.

Because the Earth's surface is relatively cool it re-emits the Sun's energy in the infrared frequency, mainly in the range 5–25 μm wavelength. Thus, atmospheric heating is largely from *beneath* and greatly increased by the concentration in the air of the *greenhouse gases*, mainly water vapour, but also carbon dioxide, carbon monoxide and methane. Water vapour may double the sensitivity of the climate to the other greenhouse gases (Del Genio, 2002). Aerosols in the upper atmosphere scatter insolation, reducing global heating, and are more effective in this than in trapping long-wave radiation from below (Soden *et al*., 2002). As they increase globally after big volcanic eruptions, this results in global cooling by as much as 0.5°C. But were it not for the atmospheric absorption of heat from below, the temperature of the Earth's surface would fall by some 40°C, making life in its present form impossible: a new aspect on global warming! Indeed, several workers believe that increased CO_2 is partially a result of higher global temperatures, not vice versa. Correlation is not causation, and students must be aware that global warming has become a political issue (Parmesan, 2006); doubtlessly global cooling would engender greater consternation! Nevertheless, it is undeniable that anthropogenic outputs of CO_2 and methane have been increasing since the Industrial Revolution (Vitousek, 1992), and are responsible for up to half of the change in greenhouse effect (Cammell and Knight, 1992). However, CO_2 comprises only 0.038% of the Earth's atmosphere (it was 0.028% in 1750), methane comprises a mere 0.0017%, while water vapour, averaging ~1% but showing much local and temporal variation, is generally *the major greenhouse gas* (Jones and Mitchell, 1991; Barry and Chorley, 1995). While cloud, according to its thickness, reflects much insolation, it also reduces the heat lost from the Earth's surface. Indeed, water vapour, while absorbing heat from this surface, emits less of it back into space if it is high and cold (Del Genio, 2002), thus warming climate. Related effects result from the dust clouds and aerosols emitted by major volcanic eruptions, such as the massive one in 535 AD, although these last only a few years (Soden *et al.*, 2002). For an informative diagram of terrestrial insolation see Odum (1971, Fig. 3.1).

Heat then, as well as light, may be reflected, but the part that is absorbed is transported around the globe in air and water masses, the process of *horizontal advection*. Air masses are advected by the effects of temperature differentials between the poles and the Equator. They may move fast, but ocean currents transfer more heat due to their immense thermal capacity, and in a sense have greater 'memory' than air masses. The UK, for example, is much milder than expected, which is due to the heat transfer provided by the Gulf Stream and the associated south-westerly prevailing winds. Without such global transfers, equatorial regions would be hotter and polar regions colder than they are now. Advection also effectively masks the 7% annual variation in insolation received due to the Earth's slightly eccentric orbit, which ought to, but does not, make winters in the Northern Hemisphere slightly warmer than those in the Southern Hemisphere. Air masses thus have hygrothermal properties that are characteristic of their regions of origin, but these are progressively modified by conditions they meet as they move. Just as advective currents carry the pelagic larvae of many marine organisms, so seasonal advective winds transport huge numbers of migrating adults of many insects.

Apart from these largely lateral transfers, there is also a global system of vertical air movement. Due to there being maximum heating from the Earth's surface around the Equator, according to season, this shifting, tropical air rises and is replaced by surface air from north and south. This forms the Inter-Tropical Convergence Zone (ITCZ). In the main it follows the position of the overhead Sun, and hence maximal heating, from the Tropic of Cancer in July to the Tropic of Capricorn in January. But there are irregularities. A northward loop in the ITCZ reaches Korea and South Japan in the northern summer and southward loops exist in South America and in Africa in the southern summer. Convergent winds into the ITCZ have determining effects on migrant insects throughout these areas.

One might expect this system to extend to the poles but, due to the peculiar dynamics of these great air masses, the equatorial air sinks again at ~30° north and south of the ITCZ. There is a similar vertical system between ~30° and ~60° latitude, in all making three segments in each hemisphere, the latitudinal vertical circulation (LVC). The falling air becomes warmer as it sinks and therefore can contain more atmospheric moisture, so that in such regions it seldom rains: mean annual precipitation (MAP) is low. There are deserts at around the 30th parallels both north and south of the Equator. These effects are *a function of latitude*, underlining the primary importance of this basic geographical factor on plant communities and their associated faunas. Temperature *ranges* too are a function of latitude, being least in the tropics and greatest nearer to the poles, while precipitation *ranges* are the opposite, being greatest at the Equator (Stevens, 1989).

Atmospheric depressions circulate clockwise in the Southern Hemisphere and anticlockwise in the Northern Hemisphere, under the influence of Coriolis Force. Moving air and water masses tend to deflect right in the north and left in the south. Coriolis Force results from the fact that a point on the Equator relative to the stationary poles moves at 1680 km/h. Points along any line of longitude move at diminishing speeds as the poles are approached. Circulating air masses are also influenced by land and water temperatures beneath them and re-directed by mountain ranges. When saturated air is forced upward it is cooled. It can contain less water vapour and rain or snow eventually fall. The LVC in conjunction with Coriolis Force also give rise to the westerly jet streams. Coriolis Force naturally dies away to nothing at the Equator, but elsewhere it affects circulating and upwelling ocean currents, although other complex dynamics operate. For example, because water is most dense at 4°C, polar waters tend to run down into profundal zones, setting up deep currents that surface in the tropics. Differences in salinity also affect this movement (Kerr, 2000). But there are even greater meanderings, and a major current circulates between the Atlantic, Indian and Pacific Oceans. Surface waters are influenced strongly by prevailing winds. The strong westerlies at around 45°S (Roaring Forties) cause the southern surface waters of the Atlantic, Indian and Pacific Oceans, modified by the shape of continental landmasses, to circulate in an anticlockwise direction. Farther south they drive the Antarctic Circumpolar Current.

All these global processes are variable on decadal and multidecadal time scales. Shifts in the temperature distribution in the Pacific Ocean and associated changes in wind patterns, drive the El Niño/La Niña (ENSO) climatic phases (Bjerknes, 1969; Cane, 1986). These occur with a periodicity of 3–11 years. It seems there is no regular cyclicity in El Niño events; rather, major oceanic and atmospheric conditions build up and are then released by some minor ones, perhaps chaotically (Cane, 1986; see also Section **11.3**). In an El Niño year, relaxation of the easterly trades along the Equator leads to warming of the Pacific Ocean down the tropical and sub-tropical coasts of the Americas. The thermocline is suppressed, the ITCZ moves unusually far south to Peru, and convectional rain falls in these normally arid areas. Farther north in the Gulf of California, rainfall was more than five times that of the MAP during the 1992–1993 El Niño (Polis *et al*., 1997a). Meanwhile, drought occurred in the Western Pacific and much of South-East Asia (Fedorov and Philander, 2000). Possibly, global warming will increase the intensity of these changes. In all, the ENSO affects the flora and fauna over a quarter of the Earth's surface.

In the North Atlantic, periodic fluctuations in air pressure between the north and south (the North Atlantic Oscillation, NAO) affect climatic patterns in North-Western Europe (Westgarth-Smith *et al*., 2005). The NAO influences oceanic temperatures and currents, while the increasing warmth of the seas around Africa may be a major cause of recent Sahelian droughts (Giannini *et al*., 2003). In turn, these droughts are associated with the transport of mineral dusts to the Americas, and have other macroclimatic consequences (Kerr, 2000; Prospero and Lamb, 2003). Such chains of effects in the Pacific and Atlantic, the dynamic interplay of atmosphere and ocean, add complexity and irregular periodicity to climate, which influence insect ecology (Pedgley *et al*., 1995). Thus, the NAO affects the migration into the UK of many Lepidoptera including pests (Sparks *et al*., 2005).

High rainfall promotes plant growth, of course, assuming temperature is not too low. Rainfall, more precisely precipitation, as dew, hail and snowfall must be included, largely influenced by the vagaries of oceanic and atmospheric circulation, varies enormously between different global regions. MAP is an incredible 10,977 mm at Cherrapunji in the Khasi Hills of north-east India, but zero at Aswan in Lower Egypt (Anon, 1997). Higher altitude tends to promote higher precipitation (Section **2.2.2.2**), but this is not universal. High up in the central Andes, for example at Socompa (>4000 m altitude), associated with the Atacama Desert, there is hardly any rain, whereas in the northern Andes at Bogota (2660 m) precipitation is >1000 mm MAP. Of course, it varies during the year. That is to say, like heat and light, precipitation has periodicity, although this is not always predicable. The monsoon season of the Indian region and the mild wet winters and hot dry summers of the Mediterranean Basin are, however, fairly predictable. Relative to latitude, the circulation of air and water masses, and the associated temperature regimes that they bring, gives any point on the Earth its characteristic climate. The term 'weather' refers to the short-term (hourly or daily) complex changes in climate (long term) at such a point.

Apart from intensity, light input from the Sun has periodicity and quality. The former, being determined by the Sun's position in relation to a specific latitude on Earth, varies predictably during the day and the year. It is a *predictable, temporal component* of weather and in the longer term of climate (Section **10.1.1**). Predictable events are critical in the ecology and evolution of life-history strategies in insects and other animals. For us, it is also useful to be able to predict pest outbreaks (Section **13.1.1**). Then, many organisms use the relative duration of day and night (photoperiod) to determine their position in the annual cycle. Light quality varies according to selective, atmospheric absorption and is influenced not only by cloudiness, but also by dust from deserts, volcanic eruptions and other diverse pollutions and the light environment (Section **10.2.3.5**).

Summarily, the drivers of climate include predictable, unpredictable and chaotic components. Latitude is the main determinant of average temperature and light intensity, and, given the presence of adequate water and nutrients, the overall rate of plant metabolism. But because of variation in altitude and the vagaries of global wind and water circulation, places at the same latitude often have dissimilar climates. Temperature and thermal radiation also affect the rate of animal metabolism. Of course, cold-blooded animals, like most insects, are more affected by these factors than are warm-blooded animals. But the climatic changes observed in our own lifetime are minor compared with those resulting from the Milankovitch Cycles or even the Maunder Minimum. The fauna and flora we observe today, or more precisely their ancestors, have survived many such events, or rather have been selected for survival in an average of all of the environments experienced (McShea, 1998). We have dealt with these global, physical processes, which are variable and often periodic on various temporal and spatial scales (Levin, 1992), in detail, as they set the stage for the biotic interactions given in Chapters **9** and **10**.

2.2.2.2 Some local, mainly constant, effects

As von Humboldt pointed out, altitude has further determining effects on physical factors. It is partly a surrogate for latitude; an increase in altitude is in some ways similar to going nearer to the poles, as there is a decrease in mean temperature. But other physical factors, especially the nature of erosion, are altitudinal effects *per se* and relate to mountainous and, to a lesser extent, hilly regions. Also, as one gets higher, insolation increases, since the atmosphere becomes thinner and absorbs less of it. So radiant energy, both heat and light, are no less. Soil surface temperatures of ~60°C have been recorded in the tundra zone of the Rocky Mountains (Watt *et al*., 2003). But air temperatures in the shade and at night are much less. The drop in mean temperature is the *adiabatic lapse rate*, maximally 9.8°C/1000 m, but as low as ~6.0°C/1000 m in high humidity and temperature (MacArthur, 1972; Barry and Chorley, 1995; Colwell *et al*., 2008). In mountainous and hilly regions, which comprises about half the Earth's land surface, the slopes may be steep, so that the insolation, depending on slope and aspect, is spread over a greater or lesser area, just as it is at different latitudes. There is also the point that the greenhouse effect reduces with altitude (Leather *et al*., 1993). The resulting extremes of temperature between insolated and shaded surfaces generate strong winds. Then the reduction in atmospheric pressure reduces the availability of oxygen. For example, at 3000 m atmospheric pressure is about half that at sea level. This reduction results in a greater rate of evaporation, one increased by the high winds, although the reduced temperature has an opposite effect. Weather in mountainous areas is different from that in the plains, and its local variation there can have marked effects on the ecology of insects. Overall, insect faunas are richer in montane areas although this is limited by increasing altitude (MacArthur, 1972).

Topography, on the majestic scale of mountains and on the lesser scale of hills, also provides shelter from winds and induces rainfall. Moisture-laden air blown over high land cools and drops rain so that precipitation in the lowlands beyond is reduced, an area called a '*rain shadow*'. In tropical mountains, maximum MAP often occurs between 1000 m and 1500 m, but in mid latitudes this band is between 3000 m and 4000 m (Sømme, 1989). In Europe, maximum forest productivity measured by litter fall is at 450–850 m (Bray and Gorham 1964). High land also influences the movement of frontal systems, which greatly effect migrant insects (Wellington, 1954; Johnson, 1969; Drake and Gatehouse, 1995). Topography determines the drainage pattern of water, the redistribution of eroded material and, consequently, the type of soil formed (below). And in the long term it is subject to change by orogenesis and erosion (Whipple *et al*., 1999). On a hillside the little valleys formed by streams support a different flora and insect fauna than those on the ridges between them.

While local topography affects ambient temperature and to an extent light, the directional aspect of hill and mountain slopes has further effects. In the Northern Hemisphere, north-facing slopes have cooler, damper microclimates than south-facing slopes. Plant communities in hilly areas are more diverse. Related to this, there are important effects on crop cultivation. The champagne grapes grown around Dijon are towards the northern limit of distribution, and are planted on slopes with a mainly southern aspect, making the most of the available sunshine. Then, east-facing slopes receive direct sunlight in the morning, west-facing ones in the evening, so producing different microclimates. Weiss *et al.* (1988) provide a detailed account on the influence of topography in the ecology of the nymphalid butterfly *Euphydryas editha*, which has general interest.

Soil type, although primarily influenced by local geology and erosion, is also influenced by topography. Soil depth, acidity, alkalinity and fertility are important determinants of plant growth (Polis, 1999). For example, soils on hill tops are often thin, stony and acid; those in valleys deeper and fertile. We often find bracken, a good indicator of mildly acidic soil, even on the top of limestone hills. Diverse physical processes produce localization of organic material and in turn greater plant diversity on a spatial scale that relates to the size of the mountains or hills. 'Climatic and edaphic factors are the basis of environmental diversity, producing not only the fragmentation of habitats but a constant change in their character and location' (Thompson, 1956).

Close proximity to the sea and big lakes tends to stabilize temperature both seasonally and diurnally (Leather *et al.*, 1993) because the thermal capacity of water is far greater than that of land. Both warm and cold oceanic currents have effects on the coastal zone. Even within several kilometres of the sea the increased wind and wind-blown salt spray have a noticeable influence on the vegetation. By contrast, flat plains distant from water masses have a wide fluctuation of temperature, more uniform soils and less plant diversity. So, two points separated by longitude do not show consistent climatic differences, as do two points separated by the same degrees of latitude (Stevens, 1989). Even slight gradients affect drainage patterns and ponds and various hollows gather wind-blown organic material, again ultimately influencing soil type and in train promoting biotic diversity (Huston, 1993). For a general account of climate and weather, see Barry and Chorley (1995).

While light affects insect distribution directly (Section **10.1.1**), it is a major factor in the distribution of plants, particularly through the influence of shade (Harper, 1977; Valladares and Niinemets, 2008). Shading may come from other plants but there is also self-shading. Light also influences insect distribution secondarily, and with respect to self-shading, insects often prefer lower, shaded areas of the plant (Section **10.1.1**). Shade tolerant plants, especially those in woodland understories, unlike those in the open, may be harmed by excessive irradiance, and although several exceptions exist, they are less likely to form extensive stands as grasses do.

2.2.3 The plant associations

2.2.3.1 General introduction

Plant associations occur on at least four spatial levels. There are major associations such as tropical rain forest, grassland and temperate woodland, which together with their faunas are termed *biomes*. A biome is '… the largest land community unit which it is convenient to recognise' (Odum, 1971). Within them one may distinguish smaller plant communities, concisely called '*biotopes*'. For example, broad-leaved temperate forest contains communities such as oak and beech woodland. We will use '*plant association*' in a general sense, 'biome' or '*global association*' for first-order and '*plant community*' or '*biotope*' for second-order associations. At a third spatial level there are lesser variations, for example, the gap phase vegetation following the fall of a forest tree. Finally, many herbaceous species form clones by vegetative reproduction. When the physicochemical and edaphic environments are added to these biotic groups the term *ecosystem* is appropriate.

There are two views as to the validity of plant associations. First, they are real entities with inclusive and characteristic properties. Second, the only real entities are the individual plants. This argument is like that of the *individual and the population* (Section **9.6**). Following Heinrich Walter (1971), we adopt some middle ground: while some biotopes are sharply defined, in others there is a gradual replacement along an environmental gradient of one plant species by others, so that species' distribution is paramount.

The biotopes described below are called *climax communities* and these, from an animal ecologist's viewpoint, are often regarded as *habitats* (Section **9.5**). How do these communities originate? If a catastrophe such as fire or landslide reduces an area to bare soil, plants soon begin to colonize it. The vegetation then passes through a series of stages (*seres*) of increasing height and initially species diversity until the final, climax community is reached. This begins when we clear an area for agriculture. The troublesome weed species represent the initial stage, leading to the climax sere. If agriculture continues, these seral changes are suppressed, but if a field is abandoned they will start as surely as night follows day. In the main, the early associations are ephemeral, comprised of short-lived plants with high reproductive potentials (*r*-selected), later on long-lived plants with high competitive ability (*K*-selected) gradually take over (Grime, 1974; see also Section **9.1**), resulting in a more stable community. Such progressions are major causes of change in habitat quality for insects (Section **12.2.2**) and other animals. But other less dramatic floral changes occur, sometimes driven by climatic changes, or today more frequently by the introduction of exotics (Section **12.2.6**).

There is a basic interaction between a plant community and the soil beneath it (White, 2006). While an oak forest and a heath may exist on the same bedrock, the soils that develop under each community are different. When these rocks are calcareous, tree roots penetrate them, and by translocating the calcium form a near neutral soil. Shallow-rooted grasses cannot do so and so the soil remains acid. These processes naturally influence the insects there, especially those, like the Tipulidae, that spend much of their life cycle in the soil.

Let us look at the global associations generally and simplistically: there will be variations both to the classification used here and between different regions in each biome. An important source of variation is that within any association. Thus, the plant species, although filling similar ecological niches, will be largely different species in different continents. For example, the trees in Amazonian rain forest, although stratified in the same way, are almost entirely different from those in Malaysian rain forest. However, exotic species, particularly weeds, cross oceanic barriers in increasing numbers.

2.2.3.2 Plant associations from the tropics to the tundra

Starting at the Equator and moving to ~15° north or south, areas with rainfall >2000 mm/yr and a minimum of ~100 mm in any month, have a climax association of tropical rain forest (*selva*; Section **12.2.2**). This is a single biome but the others are separate in Northern and Southern hemispheres, each with its own characteristics. Because of high rainfall, soils are leached heavily and so often poor in nutrients. But advective inputs of nutrients in dust, particularly phosphorus from Africa, permit the luxuriance of the Amazon Basin (Swap *et al*., 1992, in Polis 1999). These forests comprise ~1800 million ha, almost half the world's total (Nair, 2007), and contain a great variety of trees and other plants, each species being typically highly dispersed and thus at low population density (Janzen, 1970). The tropics provide the major region to generate new species and to conserve existing ones (Chown and Gaston, 2000), hence they possess great biodiversity.

The major areas are located in: (i) the Amazon and Orinoco Basins, with an extension into a high rainfall area in Central America; (ii) the Congo Basin with an extension across the Niger Delta, and in eastern Madagascar; (iii) the western coast of India (Western Ghats); and (iv) much of South-East Asia including the islands of Indonesia, Borneo, the Philippines and New Guinea. These forests are highly stratified vertically (Smith, A., 1973), with a canopy at some 30 m through which some very tall trees penetrate, plus several layers underneath. Mature forests, because of irregularities in the canopy, show considerable horizontal patchiness, with numerous tree species at different growth stages (Janzen, 1970; Chazdon and Fetcher, 1984). There are also great differences between the levels of physical factors operating in the canopy and at the forest floor. At high elevations this association becomes 'cloud forest' or 'mist forest', with a much reduced canopy height. Within the tropics, some areas have soils so poor in nutrients that they can only support grasslands, for example, in Brazil where they are known as 'pantanal'. While the latter cannot sustain any agriculture, cleared rain forest can yield maize, rice, cassava, yams, bananas and sugar cane, and several minor crops but, being low in nutrients, it is unstable. Cleared rain forest has been used for cattle ranching, an exceedingly wasteful process: short-term financial gain is swapped for long-term natural production and conservation, one having marked effects on the local climate (Uhl and Kauffman, 1990). In Brazil and elsewhere, it has been shown that a properly conserved rain forest can yield products of greater monetary value than the same area cleared (Panayotou and Ashton, 1992), so that even on a purely economic basis clearance is wasteful: an appalling case of *ignorance in action*, more likely avarice in action. In the Malaysian Peninsular, however, large areas of erstwhile forest now house rubber or palm oil plantations that seem to be stable, and worldwide there are numerous forest plantations of timber species (Richards, 1966; Leigh, 1975; Morley, 2000; Nair, 2007).

Further from the Equator, but still within the tropics, for example in the Yucatan Peninsula, Oaxaca in Mexico and Chiang Mai in northern Thailand, it is usual to find that seasonal rainfall is more unevenly distributed and the MAP is ~1500 mm. There may be one or two annual dry seasons in which the vegetation is drought stressed. Forest of this type exists in a broad band across southern Africa between 10°S and 20°S, where rain falls mainly in the southern summer. Natural and manmade fires therefore occur, and there has been natural selection for tree species that can resist them. Here a lower, less lush type of climax forest exists with a canopy height of some 20–25 m. All the above crops can be grown, although irrigation is necessary during dry weather. Forest plantations of *Eucalyptus* and *Acacia* spp. exist. Students familiar only with temperate situations should appreciate that water evaporates much faster in the tropics. Hence, while 1500 mm MAP produces a lush environment in temperate regions, in the tropics it produces one that is drier and dependent on rainfall distribution. This biome, like selva, is rich in plant species, creating a great diversity of niches for insects and other animals (Fischer, 1960; Nair, 2007). Such biomes are 'regionally rich' (Cornell and Lawton, 1992) in species, so that a large pool of potential colonists, including pests, exists for any habitat.

Where there is <1000 mm MAP, often with a marked dry season in the winter, the tropical or sub-tropical climax communities become savannah: grassland with few trees and/or thorn scrub. Again, fire is an important factor in their species composition and ecology in general. Any agriculture depends on irrigation, so that it is usual for crops to be planted near natural water, to impound water in ponds or to sink wells. In Africa this area is extensive, forming an east to west sub-Saharan transition zone between forest and desert (including arid grasslands), but also existing in other diverse areas (Pedgley *et al.*, 1995; Abate *et al.*, 2000). It contains much of the human population, but developed irrigation systems are unusual. The original staples of millet and sorghum, which are drought resistant, have to an extent been replaced by maize, cassava and bananas, which are not. The banana and its botanical cousin the plantain in particular need a lot of water and shelter if they are to bear well. Other large areas of savannah occur in Central and South America, particularly the Brazilian cerrado. Further areas of savannah occur in India and on the fringes of the Australian Desert.

In several of the biotopes noted above, a shifting agriculture (such as 'slash and burn') is commonly practised. An area is used for cropping and then abandoned. This has the biological effect of increasing the complexity of the vegetation, since all the seres leading to the climax one may be present within a limited area, harbouring a great variety of insects, both harmful and beneficial, which can affect crops and livestock.

The great deserts of the world occupy sub-tropical or warm-temperate regions between about 15° and 40° from the Equator and have <250 mm MAP. Alice Springs in the heart of Australia on the Tropic of Capricorn has 253 mm MAP. Recall (Section **2.2.2.1**) that this is the general region in which descending air from the LVC occurs. But rainfall is highly variable between years (Barry and Chorley, 1995), and so the main driver of primary production. Together with adjacent arid grasslands and scrub (*Sahel*), deserts comprise some 30% of the world's land area, ~170 million km^2. The major desert system embraces the Sahara, the Arabian Peninsula, parts of Iran, the Thar Desert in Pakistan, and an extensive area north of the Tibetan Plateau abutting on the steppes and including the Taklimakan and Gobi Deserts. Then in South-West Africa there are the Namib and Kalahari Deserts. About half the area of Australia is desert. In the New World the part of Chile to the north of Santiago comprises the Atacama, while in the west of Argentina there are extensive areas of salt desert where rivers draining the slopes of the Andes evaporate. In North America we note the Mojave Desert of south California and the Sonora Desert on the Mexico/Arizona border.

Paradoxically, desert topography is sculptured by rainfall. On the rare occasions when heavy rain falls there is massive erosion since there are few plants to bind the soil. Even so, blue-green algae, cyanobacteria and fungi in some areas form a barely perceptible 'crust' that helps to stabilize the sand (Zaady and Shachak, 1994). Wind erosion has a more constant but superficial effect, producing shifting dunes. Higher desert plants are either perennial and highly adapted, such as the New World Cactaceae, the Aizoaceae of Southern Africa and the amazing strap-leafed gymnosperm *Welwitschia* of the Namib Desert, or *therophytes*, which exist only as seed banks during the prolonged droughts but grow rapidly after rain. Crop plants can be sustained in deserts if they are continuously irrigated and this is normally feasible only around oases or close to large rivers, as for example along the Lower Nile. Deserts vary according to soil, rainfall and whether rivers flow into them and then evaporate leaving a saline desert, as in the west of Argentina. Various types of cactus/thorn scrub and/or tropical grasslands may be found on the fringes of these deserts.

In Israeli deserts, the high level of capital investment, human expertise and commitment make more sophisticated forms of agriculture feasible. But there is a sting in the tail. When irrigation water evaporates it leaves behind the salts it contains, and may also draw up salts from deep in the soil, leading to increasingly saline surface conditions (Section **10.1.1**). A similar problem occurs in California, and more extremely in Uzbekistan, where the Aral Sea has been drying up due to using its feeding rivers for cotton irrigation (Stone, 1999). Another unfortunate consequence of irrigation in such areas is that it frequently leads to an expansion of mosquito populations (Pennisi, 2001), with an increase in malarial and arboviral cases (Section **7.3.2.4(d)**). Around the Aral Sea locust plagues have developed (Section **5.2.1.1(b)**).

Mediterranean vegetation with its extension into the 'Fertile Crescent' of Anatolia and northern Iraq has been highly modified, since civilizations have been there for a long time (approaching 10,000 years). So long, in fact, that the climatic changes mentioned above, including those due to shifts in the spatial relationships of the Earth and the Sun, have occurred. In particular, there has been a drying out of the North African coastline. Essentially, it is a transition zone between desert and northern hardwood forest. There is typically 400–800 mm MAP and a climate of mild, wet winters and hot, dry summers. The vegetation comprises evergreen trees and shrubs (Myers *et al*., 2000). These hot summers lead to natural fires that have a big effect on the climax community and the insect fauna. Some trees, such as cork oak, have thick, insulative bark (the cork's function), while others store reserves in underground roots and tubers and can regenerate rapidly after fire. The canopies of many Mediterranean trees, like some in the tropics, are parasol-shaped, so intercepting maximum insolation from above (Horn, 1971; Terborgh, 1985). Wheat and barley originated here, and their seeds, which naturally had to resist the hot summers, are easy to store. Grapes (for wine), citrus, olives, cotton, maize and numerous vegetables, especially tomatoes, peppers and aubergines, are grown. Similar vegetation is found in California (Chaparral), central Chile, the Karoo and southern Australia. Go to your local wine shop and look at the labels!

Temperate broad-leaved, deciduous forest (hardwood) is variable in its latitudinal distribution due to the effects of warm and cold ocean currents, but 35–60°N are rough limits. There is ~600–1200 mm MAP. In Europe, winters are milder in the west due to the warm Gulf Stream, but much colder in the east due to the effect of the huge Eurasian landmass. Here most forests on flat land have been cleared and the remaining natural woodlands are often found on steep slopes unsuitable for agriculture. Look at a map of Shropshire in the west of England to see what I mean. In addition, the remains of oak forests, the wood used to construct sailing ships, persist near the sea in some places. In England, wooded parks were established from 1500–1900 thus reversing the ongoing demise of woodland habitats (Hoskins, 1955). As usual, France is better provided for. The major crops are wheat, maize, sunflowers (oil), grapes, peaches and apricots in milder areas, and wheat, oats, barley, flax, rapeseed (canola oil), sugar beet, apples, pears, plums and cherries in cooler regions.

The centres of the great northern continental landmasses have ~300–800 mm MAP, extremes of summer and winter temperature and are characterized by grasslands. Sometimes these are divided into *prairie*, in which tall grasses dominate and *steppe*, in which short grasses do so. They often fringe the northern deserts, but an extensive area of tropical grassland occurs to the immediate south of the Sahara. Smaller areas of grassland occur in the Southern Hemisphere, the main ones being in Argentina (pampas), Australia (the outback) and South Africa (veldt). They are regions for raising cattle and sheep, indeed Owen (1980) has held that the existence of grasslands is generally dependent on grazing mammals: rather like mowing being essential to maintain a good lawn. Even so, much more energy transfer occurs below ground than above it (Section **8.2.4**; Stanton, 1988). These areas contain many C_4 grasses (Wand *et al*., 1999), often living in mutual association with fungal endophytes that enhance their growth and may deter grazing from insects and mammals (Clay, 1990). In temperate grasslands, however, wheat and sunflowers may be grown where water is available.

Immediately to the north (50–70°N) of the grasslands and broad-leaved forest there is the extensive northern coniferous forest or taiga (pronounced ‘tiger’). South of the taiga a transitional zone of mixed deciduous and coniferous trees exists in some regions, in which the conifers tend to grow on the ridges and the broad-leaved trees in the valleys. The only crops here are the trees themselves, although small, cleared areas may grow barley, grass (hay and silage) and a few vegetables, as in Scandinavia. This association is poorly represented in the Southern Hemisphere because the land area at these latitudes is small. Relative to tropical forests, temperate broad-leaved and coniferous forests are poor in plants. Typically, a hectare of such forest contains only 10 to 20 species of trees, whereas in tropical forest this diversity could be a hundred times as great, with consequent effects on the regional richness of insects (Section **2.3.1**). Conifers here are tall and columnar, thus intercepting insolation from the side (Horn, 1971; Terborgh, 1985), as the Sun is never high in the sky. Trees do not grow where the mean temperature in the warmest month is <10°C. This useful rule of thumb defines an extensive band of tundra, the ‘Arctic Desert’, north of the coniferous forest. All plants may suffer from ‘frost drought’, for the ground is permanently frozen in most areas although the surface melts during three or more summer months. While topography influences the vegetation, most of the zone is unsuitable for agriculture and therefore of small interest for our purposes, excepting that the Laps graze their reindeer there.

There are several more local plant associations than those considered above. Montane environments produce a variety of biotopes, while acid and alkaline drainage systems have marked effects upon the local flora. There are big areas of acid bog and moor and some marshland. Of the ~560 million km^2 of the Earth’s land area, only ~68 million are arable, often producing cereals, but pastures and rangelands take up ~34 million more and ~24 million, respectively, are orchards and vineyards. Human habitation occupies <3 million km^2. Deserts, the Antarctic Ice Cap, mountains and forests comprise much of the remainder. Students should see MacArthur’s (1972) original book *Geographical Ecology* and Colinvaux’s (1986) very readable text.

2.3 Classifying Plant Pests

2.3.1 General introduction

The herbivory of terrestrial plants is not a simple matter. These plants proceeded to evolve some 70 Ma before herbivorous insects started to make inroads on their biomass (Southwood, 1985). One route, taken by the Orthoptera, was via saprophagy, the consumption of decaying plant material, the other involved eating fallen pollen, ending up with insects living in the strobili of Pteridophytes and early Gymnosperms, probably in the lower Permian (Malyshev, 1968). The genesis of the Hymenoptera from the Mecoptera was possibly by pollen eating. The most primitive sawflies, the Xyelidae, feed on pine pollen. In the Carboniferous, coprolites (fossilized frass) often contain both spores and pollen (Scott *et al*., 1992). Herein lies the origin of the pollination syndrome that developed considerably with the evolution of flowering plants in the Jurassic (Section **8.2.1**). But the general onset of plant feeding was resisted by development of secondary, defensive plant compounds (Section **2.4.2.**) and by symbiosis with bacteria by the herbivores. Southwood further suggests that these ‘biochemical brokers’ were essential at the inception of herbivory, as indeed they often are today. Such bacteria detoxify defensive compounds and provide essential nutrients for the insects (Section **10.2.2.6**). More recently it has come to light that plants, too, may employ rather cryptic symbionts for their own defence (Omacini *et al*., 2001). Although the role of fungal mycorrhizae has been known for a long time, their major importance in promoting plant diversity has being appreciated only recently (van der Heijden *et al*., 1998).

More than half of all known species comprise terrestrial plants, their herbivorous insects and their enemies (Strong *et al*., 1984). Then again, >50% of described insects are herbivores (Price, P.W., 1997). But they are confined to a few orders. In exopterygotes, herbivores exist almost exclusively in the orthopteroid complex and in the Hemiptera, while in endopterygotes only the four large orders (Coleoptera, Hymenoptera, Lepidoptera and Diptera) contain them, although the Hymenoptera have a high proportion of parasitoids and predators. These are the only six insectan groups that each possess >10,000 described species. In all, >400,000 herbivores have been described, and Mitter *et al*. (1991) suggest that herbivory itself often leads to speciation and hence greater diversity. Since herbivores today feed mainly on Angiosperms, the expansion of this group at the end of the Cretaceous must have brought about their considerable increase and diversity (Section **1.3**). Estimates are that each plant species is associated with a mean of around three insect species, although some large, common trees have many more. Note that Angiosperms, with >250,000 described species, have much greater variety of growth form (Raunkaier, 1934) than that of any plant group preceding them: trees, shrubs, herbs, vines, aquatics and parasitic plants. The Gymnosperms, with only ~750 world species living, are almost exclusively trees and shrubs. Diversity builds upon diversity, the law of increasing complexity (Huxley, 1942).

We have seen that insect diversity as well as plant diversity is affected by latitude. Most insect groups are more diverse towards the tropics, particularly because the herbivores have far more plant species to feed on. In the tropics, each species of tree supports a mean of 23.5 species of leaf-eating insects/100 m^2 of foliage, but in temperate forest the estimate is 29.0 species/100 m^2 (Novotny *et al*., 2006). So, insect diversity is driven largely by plant diversity, which overall is five to ten times greater in the tropics than temperate regions, even more so in selva. Also, the rate of predation, mainly by ants, on herbivores is much higher in the tropics. Then, some groups are largely tropical. Mantids, termites and most swallowtail butterflies have a mainly tropical and sub-tropical distribution. But aphids, sawflies, ichneumons and burying beetles (Silphidae) are mainly temperate.

2.3.2 An ecological classification of plant pests

Herbivory is the primary link between autotrophic production and heterotrophic consumption. It occurs above and below ground. The way insects distribute eggs (*egg distribution*) across food plants affects the structure of a web of interactions among these plants, herbivores and the enemies of herbivores (Ohsaki and Sato, 1994). Plant pests are 'grazers', showing various degrees of specialization. Thus, the part of a plant they attack forms the basis of an informative ecological classification. Groups that feed similarly, such as sap suckers, form a *feeding guild* (Root, 1967, 1973). The term comprises species without regard to taxonomic affinity and relates to our ecological classification of pests: a guild attacks *the same plant species in the same way* (Jaksic, 1981).

In successive chapters we will deal with the following pests, *some* of which are guilds:

- Chapter 3 – pests within the soil, attacking roots, tubers and sown seed;
- Chapter 4 – pests of woody and of soft stems;
- Chapter 5 – pests of leaves, leaf buds and stem apices; and
- Chapter 6 – pests of flowers, fruits and seeds, including those in store.

While a large majority of pests attack a single plant organ system, validating our classification, a minority is found on more than one system. If so, the pest will be listed under the heading of the marketable product attacked. Rarely do pests that feed on plant organs below ground also eat those above it. Locusts, when ravenous, however, will eat almost anything organic they can lay their mandibles on (Section **5.2.1.1**), chewing plant tissue down into the ground. But in several endopterygotes, especially beetles, larvae and adults feed on different regions of the same plant. In the citrus weevil *Exophthalmus* (Section **3.2.2.1**(**b**)), the vine weevil *Otiorhynchus* (Section **3.2.1.2**(**c**)) and flea beetles such as *Phyllotreta* (Section **5.2.1.2**(**e**)), the larvae eat the roots and the adults eat the leaves. In a few exopterygotes too, such as cicadas and cercopid bugs, nymphs and adults feed like this. But several Chrysomelidae, such as Colorado beetles (Section **5.2.1.2**(**c**)), are exceptional in that the adults and larvae feed together. The aphids *Pemphigus* (Section **3.3.3.1**(**a**)) and *Eriosoma* (Section **4.3.2**), and the potato moth *Phthorimaea operculella* (Section **3.2.2.1**(**f**)) provide complex cases. But overall this classification is robust.

The classification also relates to the variable nutritive value of different plant parts. The absolute range is 0.03–7.00% nitrogen dry weight (dw) (Mattson, 1980b), a range of over 200-fold. Organic nitrogen is high (3–7% dw) in actively growing tissues such as stem apices and unfolding leaves or in storage organs like bulbs, corms and tubers, and within seeds. When tissue growth stops, nitrogen content falls sharply. Nutritive value measured as %N dw has clear patterns of variation in space (organs) and time (season) in a given plant. Consequently, much heterogeneity exists *within a single plant* as it constitutes food for insects. First, there is *sectoriality* that results from the radial organization of the vascular system, so that, say, a branch on the south side of a bush is interconnected mainly to roots on that side. Most dicots are thus compartmentalized into a series of integrated physiological units (Orians and Jones, 2001). Sectoriality is less clear in monocots (Watson and Casper, 1984) and in young plants. Second, there are big differences between the constituent organ systems (the basis of our pest classification). Third, extrinsic physical factors such as light, temperature and soil nutrients also have effects. Finally, there are biochemical consequences due to any previous attack by other pests, although these again are affected by sectoriality. Also, there is much variation *between species and groups*, for example, foliage of Gymnosperms generally contains less nitrogen than that of Angiosperms. This heterogeneity has to be taken into account when sampling insects from a plant (Southwood, 1978).

This classification also reveals that damage has normally a characteristic physiological cost to the plant, although the fact that typically only a single organ system is attacked lessens the impact. Root pests attack the plant's anchorage, water and nutrient absorption and food storage systems. Stem pests attack its transport and support systems. Leaf pests attack the plant's factories, while those of flowers and fruits attack its reproductive system. Even so, severe damage to one part of a plant will often affect the functioning of the other parts (Crawley, 1989), being mediated via the vascular pathways. In general, the reproductive output of fruits and seeds will be compromised. But plants have considerable powers of regeneration, often having reserves that are unavailable to a specific pest. Insects may also affect the population dynamics of natural plant populations, although much work needs to be done on this important aspect of ecology (Crawley, 1989). In this connection there are several cases in which insects have been used to control weeds (Section **8.2.3**).

2.3.2.1 Pests of roots, tubers and sown seed

When insects attack these structures they do so within the soil, thus producing similarities in their ecology and in the methods used to control them. Their presence is usually detected by their effect on the visible portion of the plant except, of course, when a root crop is raised at harvest, which is not the time to find out. Whether they are generalized or specialized, attacking a broad or narrow range of crops, is also significant ecologically. Generalized pests are often still present in the soil to attack a new type of crop if it is planted in the sequence of crop rotation. Specialized ones cannot do this, although all pests may immigrate from adjacent areas. But immigration contains an element of chance, whereas carry-over in the soil always has effects on subsequent susceptible crops. Pests in the soil can attack plants all year round in warm climates and also in temperate ones if the winter is mild, and are thus comparable with pests of woody stems. While their feeding is then slow, plant growth is also slow, and the plants may be seedlings, for example, winter cereals. Further, their feeding may induce the production of chemical defences by the plant, and these may lower the quality of food for other pests (Bezemer *et al.*, 2003). Generalized pests always have alternative food present either as the roots of weeds or as decaying plant material, contrasting them with more specialized ones, which generally have more seasonal food. In addition, the soil provides insulation from physical extremes, particularly low temperature and dryness, although flooding is often fatal to them. In common with many stem borers, root feeders are generally less heavily parasitized than exposed insectan pests (Gross, 1991). Almost all pests that attack roots do so in field crops. We will note the minor exceptions as they arise.

2.3.2.2 Pests of stems

These pests often operate internally and therefore, like most root pests and those of flowers and fruits, are largely hidden from their enemies and from us, although their presence is sometimes detectable from bore holes, or by sawdust-like traces of their chewing. Stems are either soft and usually annual, or woody and perennial. Soft stems are normally in fields, while woody stems are in orchards and forests, giving further weight to our classification. Pests within soft stems are often detectable by the stunting they cause and by yellowing of terminal shoots. The insects that attack woody stems internally are mainly beetles and a few moth larvae, while those that attack soft stems are usually larval sawflies or cyclorrhaphan flies. All internal pests have biting mouthparts, of course, although those belonging to most fly larvae are highly modified.

Woody stems themselves comprise two rather different environments: a relatively nutrient-rich, living phloem/cambium complex and nutrient-poor, dead heartwood, the result of secondary thickening (Section **4.1**). Life cycles are typically short in the former situation but may be up to 5 years in the latter. As with roots, a thick, woody stem provides a buffer against physical extremes, lacking in a thin cereal stem, especially so for temperature. Further, soft stems are always of short duration, so that the life cycle of pests in them must also be short. In temperate latitudes feeding is confined mainly to spring and summer. But hollow stems that die in winter and form a natural refuge are often frequented by a diapausing stage, as in *Cephus* (Section **4.4.1.1(b)**). External pests of stems generally belong to the Hemiptera and hence have sucking mouthparts. There are relatively few of them on woody stems, but when they attack soft stems they usually concentrate their attention at the apices, although scale insects are usually more generally distributed.

2.3.2.3 Pests of leaves

Pests of leaves are unusual as most of them feed externally. Leaf miners are an exception, however, and tortricid caterpillars often roll up leaves for protection. While leaf tissue is available for much of the year, according to region, most pests attack young leaves. These are richer in nutrients, particularly proteins, and often lower in toxic compounds than are mature ones. Preferred leaves are more abundant in temperate springtime and in, or just before, tropical rainy seasons. Indeed, not all leaves are of equal value either to the plant or to a herbivore. Leaf productivity is greatest shortly after the young leaf has fully expanded, thereafter gradually tailing off. Soil nitrogen affects their growth rate, their quality as food, and also where the most nutritious ones are found. In general, it seems that the best leaves are found farther from the apex in fast growing shoots and nearer to the apex when growth is slow. In the tropics, tree leaves commonly last for more than a year, a feature also found in most conifers. Leaf pests live in all ecological situations (i.e. in forests, orchards and fields) and their exposure means that they and their food can be sprayed directly with an appropriate insecticide or other formulation if other methods fail (Section **13.2**). Even so, several pests, such as Colorado beetles and diamond-back moths, are now very resistant to insecticides. In general, pests of other plant parts can be controlled chemically only in that part of the life cycle in which they are exposed, for example, when the females are laying eggs, as the plant's tissue provides an effective shield.

2.3.2.4 Pests of flowers, fruits and stored products

Again, these insects are mainly internal feeders. The internal micro-environments they inhabit, like those within woody stems, often have a poor supply of oxygen. As with root and stem pests we usually find that it is the boring larvae, with their relatively low metabolic rates, not the adults with their higher ones, which are damaging. There are two points to note. First, most flowers, and hence their pests, are seasonal and therefore present briefly, particularly in temperate regions. Pests of spring flowers, for example, those affecting orchards, often have a period of summer diapause extending through the non-flowering season. Less often, the non-reproductive adults feed on alternative foods. Further, reproduction can be intermittent between years, providing a very variable resource base, as in male cone production in balsam firs (Section **5.2.1.4(c)**) and pine cones for *Conophthorus* beetles (Section **6.3.1.1(c)**) and beech mast. Second, because the developing tissues are disrupted, there is a carry-over of damage from flower to fruit. These pests are mainly important in orchards, gardens and field crops but there are several, particularly in the 'Microlepidoptera' and Coleoptera that attack stored products. Jones and Jones (1984) and Pedigo (1996) give useful compendia of temperate pests, while Gray (1972), Hill (1983) and Speight and Wylie (2001) deal with tropical ones. Nair (2007) considers pests of tropical forests.

2.4 Herbivorous Insects and Plant Defences: An Introduction

We examine this subject in detail here since the next four chapters concern the depredations of pest insects on crops, forests and stored products. There is a huge literature on this subject, and there is a basic difference of opinion on how diverse herbivores come to be distributed on the many plant species, including crops, which they attack. We saw in Section **2.3.1** that they are confined largely to only six major insect groups: the orthopteroid and hemipteroid orders in the Exopterygota and the Coleoptera, Hymenoptera, Lepidoptera and Diptera in the Endopterygota. Then the plant species affected are largely ~250,000 Angiosperms but only ~750 mainly coniferous Gymnosperms. Crop plants, however, are confined almost exclusively to a few families (Section **2.1**). Recall in Section **2.3.1** that >50% of all known species on Earth comprise terrestrial plants, their herbivores and their enemies.

A generally held early theory is that insect–plant relationships are a product of co-evolution (Ehrlich and Raven, 1964; Feeny, 1976; Rhoades and Cates, 1976; Section **2.4.1**). But several other authors (Jolivet and Petitpierre, 1976; Jermy, 1984; Stamp, 2003b), seek causes other than co-evolution (in its strict sense; Section **8.2.1**) to explain these relationships. Therefore although plants defend themselves directly by physical and chemical means and indirectly by being attractive to the enemies of herbivores (Thaler, 2002; Ode, 2006), co-evolution may form only a part of the system. At the base of plant defence there are specific *R* genes that code for various types of resistance (Kaloshian, 2004), both to insects and to pathogens. For insects, there are three basic facts to incorporate in this mental jigsaw. First, herbivorous insects consume little of the terrestrial plant biomass. Second, the nutrients they require could be supplied by a much wider range of plants than they actually use (Dethier, 1954). Caterpillars in particular eat a much wider variety of plants in culture than they do in nature (South, 1920/1923). Third, plants possess a wealth of defences: structural, physical, chemical and ecological. They form a heterogeneous environment that changes in time and space during development, and a medium in which diverse interactions between herbivores, their enemies and pathogens occur (Stout *et al*., 2006).

Before we continue, however, we must consider briefly various behaviours insects use to locate their food plants, since this too is relevant. On a wide spatial scale, adults often migrate first and then engage in an appetitive search within a more limited arena (Section **10.2.4.1**). Apart from its other functions (**13.3.2.3**), migration also *results in* searching on a wide spatial scale, although flight is undistracted until major displacement is over (Johnson, 1969). Only then does the appetitive phase begin. For example, when *Nilaparvata lugens* (Section **5.3.1.2(d)**) migrate each year from mainland Asia to the Japanese Islands, the survivors begin to locate paddy fields, rice plants and feeding sites on increasingly fine spatial scales. After migration, insects may use topographical clues and other visual features, including apparency, plant shape and spectral emission, often employing *olfaction* at closer range. Finally, they taste plants (*gustation*) and are affected by feeding deterrents or by stimulants. A range of mechanisms has evolved to locate plant resources, from searching *en masse*, as in aphids, to an *individual ability* to locate multiple, well-spaced plants, as in hawk moths (Section **10.2.4.1**). Some plants are hard to find because they are small and/or have a low density in the landscape, with hawk moths often specializing on such resources. Juveniles almost always search on a restricted ambit. Then there are the effects of associative learning and olfactory conditioning. For example, *Manduca sexta* raised on tobacco are more likely to select that plant as adult females than alternative Solanaceae on which their progeny could thrive (Jermy *et al*., 1968).

Insect damage may result in reduced plant fitness, a necessary criterion for co-evolution. Plant fitness, while relative, is mediated through both the female and male lines (Strauss, 1997). The female part is measured in seed number and weight borne by *individuals*, the male part measured in the *total number* of seeds sired by pollen *from individuals*. But plants have evolved a complex battery of defences that are often assumed to have metabolic and other costs (Section **2.4.2**). Students should abandon the idea that just because plants do not move around like animals they are simple. One assumes that in evolutionary time the cost of plant defence has been less than that of capitulation. In forests at least, insect herbivory may have regulatory effects on primary production (Mattson and Addy, 1975). In fields we note that crop losses can be great as natural plant defences have often been compromised during plant breeding and because insecticides have been used too lavishly.

Assuming that most plants do defend themselves, however, they may delete something that herbivores need, or on the other hand evolve to dish them up with something harmful (Section **2.4.2**). Plant leaves, for example, are organs of photosynthetic production; they are not designed to be eaten by herbivores. In fact, they are designed *not* to be eaten by herbivores (Strong *et al*., 1984; Polis, 1999; Rasmann *et al*., 2005). Comprised of poorly digestible fibre and cellulose, like most of the plant, they may be further protected by physical barriers, digestibility reducers and toxins. They may also employ deception and the *indirect* forces of other organisms, their mutualistic protectors (Janzen, 1966, 1988; Thaler 2002; Ode, 2006; Holland *et al*., 2009; Section **8.2.1.2**). And when we come to consider entomophagous insects (Sections **8.2.2** and **10.2.3.9**), we will find that they employ many similar means of searching for potential insect victims as herbivores employ to find plants. Herbivores have several comparable defences to those of plants, sometimes because their chemical defences are derived from them in the first place. Indeed, tritrophic interactions (‘*tritrophisms*’) are common

(Price *et al.*, 1980; Karban and Baldwin, 1997; Havill and Raffa, 2000; D'Alessandro *et al.*, 2006; Ode, 2006).

2.4.1 Insect groups and the plants they eat: Co-evolution or not?

We consider here if the co-evolutionary model of Ehrlich and Raven (1964) explains fully the distribution of herbivores among the plant species they eat. As above, insects must find their preferred plants both in space and time. For spatial effects: small, scattered plants, like many tropical orchids, must be more difficult for herbivores to locate than large, long-lived ones, such as stands of conspecific temperate trees. For scattered plants, does their strategy represent a means to avoid herbivory? Indeed, rare plants support fewer herbivorous species than abundant ones do (Southwood, 1961). This hide and seek principle is illustrated during biocontrol of *Opuntia* cactus in Australia by *Cactoblastis* (Andrewartha and Birch, 1954; see also Section **8.2.3**). At first, great areas of cactus were eaten out by this moth; presently, the scattered remnants are ultimately found. Meanwhile, further isolated propagules take root elsewhere (Section **13.2.4.6**). And so on. A situation such as this could well be co-evolved. Conversely, we see why extensive crop monocultures are vulnerable to insect pests. Massed together they provide large, numerous targets with high '*apparency*' (Feeny, 1976), a concept combining spatial extent, biomass, visibility and chemical attraction. Such crops are often cultivars of natural plants that occurred in scattered patches (low apparency) in early succession: they did not form extensive monocultures (Price, T., 1997). While insect pests differ greatly in their powers of searching (Section **10.2.4.1**), we expect the worst when crops are grown extensively. Note again that when insects like aphids search *en masse*, very few find the resource. But in those like hawk moths, each individual usually finds many resource items.

Herbivores may be *polyphagous*, *oligophagous* or *monophagous*. Polyphagous species consume a wide variety of plants in many genera and several families. Oligophagous insects confine their depredations to a single family or even genus and monophagous ones to a single species (Fraenkel, 1959; Wäckers *et al.*, 2007). Some monophagous insects feed on a single plant species in one place but only on another elsewhere. In the first two classes, however, some individuals consume more than a single plant species during their development. Thompson (1988) calls them *grazers*. They occur more commonly in exopterygotes than endopterygotes (Dethier, 1954), for example in Dermaptera, locusts, mole crickets and some pentatomid bugs, but also in several lepidopteran caterpillars (Section **2.4.2**). Appropriately, exopterygotes have a greater number and variety of chemoreceptors than most endopterygotes do. Polyphagy is probably primitive and oligophagy derived (Brues, 1946; Dethier, 1954; Price, T., 1997), although we expect their dynamics to be complex (Section **12.3.3.1**). Even so, polyphagy indicates that the herbivore can recognize a variety of plants as food, and combat whatever diverse defences they marshal. Also, within many species several plant-specific races occur, although one must be sure that cryptic species (Section **1.3.4**) are not involved. These terms can also be applied to carnivores and parasitoids.

In Section **9.8** we consider resources such as plant food and in Section **10.2.4.1** we examine the diverse mechanisms insects use to find them. Indeed, the *evolved pattern of search* for plants may be a factor in the range of plants insects eat (Bernays and Graham, 1988). Long ago, Lovell (1914) suggested similarly that the ability of bees to find specific plants and collect pollen and nectar rapidly from them is a driving force in the evolution of oligolecty. Familiarity breeds efficiency, as in factory mass production.

The co-evolutionary hypothesis of plant defence and herbivore response has severe limitations. Jermy (1984) cites many families in which related, oligophagous insects consume distantly related plant species. Although co-evolution may occur initially, insects may change to new, unrelated food plants periodically, as in bruchid beetles (Section **6.3.1.2(b)**). Even so, in this family there is a strong link between beetle and legume taxonomy (Southgate, 1979) as there is in some psyllid genera such as *Aphalara* (Polygonaceae) and *Psyllopsis* (*Fraxinus*) (O'Connor and Malumphy, 2011). But the case of *Rhagoletis* (Section **6.3.1.1(m)**) clearly illustrates diversity. While five species of the suavis group feed on walnuts (Juglandaceae), two of the four cingulata group feed on Rosaceae and the other two on Oleaceae. Then in the pomonella group, one feeds on Rosaceae, another on Ericaceae, a third on Cornaceae and a fourth on Caprifoliaceae (Bush, 1969). Even in endopterygotes, which tend towards oligophagy, there are broadly polyphagous species, such as in several moths (*Heliothis*, *Lymantria*, *Maruca*, *Orgyia*, *Trichoplusia*; see Section **12.3.4.4(d)**), cases that are hard to explain by co-evolutionary theory. Note that the link between plant taxonomy and plant chemistry (Schultz, 1988) is a further imponderable.

Small changes in the insectan nervous system, both peripheral and central, can produce large changes in the range of food plants accepted, simply by altering the level of sensitivity to deterrents (Bernays and Chapman, 1994; Chapman, 1999). The evolution of new species may be related to simple neural changes. Overall, there are rather few cases of related herbivores feeding on groups of related plants, although kermestid scale insects on the Fagaceae (Eastop, 1978), *Conophthorus* beetles on *Pinus* (Mattson, 1980a), the bruchid genus *Caryedon* on the seeds of leguminous trees, and the chrysomelid genus *Phyllobrotica* feeding on the labiate genus *Scutellaria* (Mitter *et al.*, 1991), all do so. But the fact remains that many plants are very toxic. Plant chemistry is a major factor in the evolution of herbivorous diets (Schultz, 1988).

Temporal effects also exist. Annuals grow for only part of the year; perennials exist for several years, making them individually more apparent. Conifers, evergreens like holly and box, and many tropical trees keep individual leaves for more than 1 year and generally have a higher biomass density of foliage than deciduous forests do (Tadaki, 1966, in Mattson and Addy, 1975). Apparent deciduous trees, like birches and oaks, burst their buds rather late, thus partially avoiding spring herbivores. This may well be co-evolved, and should carry a metabolic cost as the period favourable for photosynthesis is reduced. Other reasons for such trees coming into leaf later are that most are wind pollinated, a process likely to be more efficient on leafless trees (Section **8.2.1**), and that it avoids occasional damage by late frost. There is also a scattering of bud burst times between conspecific trees, making it more difficult for herbivores to adapt the timing of their life cycles, a plant example of den Boer's principle of risk spreading (see Fig. 5.6 and Section **9.7**). Also, when insects seek flowers as food for their progeny this period may be brief (Section **6.2**). In effect, some plants have evolved to be unpredictable sources of food. Further, in some tropical trees, such as mango, different sections flower at different times. In some broad-leaved trees multiple meristems occur, resulting in genetic mosaics on the same individual (Whitham and Slobodchikoff, 1981), and hence a given herbivore may be able to adapt to only a part of it. While co-evolution explains some of the relationships between plants and their herbivorous insects, it does not explain all of them.

2.4.2 Physical and chemical defences

The physical defences of plants against mammals, such as bark (Nicolai, 1986), thorns and spines, are familiar, while those against insects are less obvious. They are largely pre-existing or passive (Kaloshian, 2004) types and include the presence of silica (Massey *et al.*, 2006), tissue hardness, a thick waxy cuticle and the possession of trichomes. Trichomes may prevent insects settling and, in addition to their physical properties, may be broken, releasing defensive compounds including repellents (Gibson and Pickett, 1983). Leaf shape also has an effect. In those that are finely divided, such as in ferns and legumes, leaf mining is effectively precluded as larvae generally cannot leave the leaflet that provides insufficient food. The resins, gums and cuticular waxes produced by several plants can be defensive, but may contain protective chemicals too. Such pre-existing defences are better developed in the tropics (Coley and Aide, 1991, in Schemske *et al.*, 2009).

Colour may also be a physical defence. Red objects are not visible to most insects, with the exception of several butterflies and a few Symphyta, as it is outside their visual range (Hinton, 1973; Briscoe and Chittka, 2001). Young foliage and many fruits are often reddish (Section **10.2.4.4**). Occasionally, plants engage in mimetic deception involving morphology. *Passiflora* spp. bear green or yellow structures resembling eggs that deter oviposition by *Heliconius* butterflies (Williams and Gilbert, 1981). Some crucifers, *Streptanthus* spp., bear red, egg-shaped structures on their leaves. *Pieris sisymbrii*, which in all probability can see red, does not oviposit on such species (Shapiro, 1981) although in the laboratory its larvae can feed on them successfully (Section **10.2.4.7**).

Defensive plant metabolites are directed against neighbouring plants, pathogens and herbivores, and as noted, their production is expected to bear a cost. This simple scenario is complicated by several factors. First, there can be no cost unless the metabolic machine is *constrained* (Haukioja, 1980; Mole, 1994). Thus deficient nutrient supply would constitute an *external constraint* and metabolic limitations an *internal constraint*. Many presumptive defensive compounds in plants, especially those based on nitrogen, are not simply dead-end pathways, but have the added function of a metabolic store (Berenbaum, 1995), and other uses have been mooted for them (Chew and Rodman, 1979, in Jermy, 1984). They are often interconvertible (Robinson, 1974; Mattson, 1980b), like insectan antifreeze (Section **10.2.3.3**). But if metabolites are locked fully in defence they cannot be used for other functions at the same time. Plants also employ symbiotic organisms, particularly endophytic fungi, in their own defence (Clay, 1990; Omacini *et al*., 2001). Indeed, typically they provide a medium in which many species (herbivores, pathogens and parasitoids) play *selfish* roles, both above and below ground: a veritable interaction web (Hatcher, 1995; Van der Putten *et al*., 2001; Forkner *et al*., 2004; Stout *et al*., 2006).

Plant defences, co-evolved or not, act against herbivorous insects either directly, or indirectly by attracting or otherwise affecting the latter's enemies (Thaler, 2002; Forkner *et al*., 2004; Harvey *et al*., 2005; Karban *et al*., 2010), and often both. In general, we expect that apparent, slow-growing plants should allocate metabolic reserves preferentially into defence and hence be *K*-selected, while those that put them into rapid growth are *r*-selected (Grime, 1974; Cates and Orions, 1975; Feeny, 1976; Herms and Mattson, 1992; Section **2.2.3.1**). Some plants are attacked by many insect species, and so may have poor defences; others are attacked by few, when the converse should be true. Overall, plants are high in carbohydrates and low in nitrogen (Southwood, 1973, 1985; White, 1993; Berenbaum, 1995), making them less than ideal food (Section **2.4**). But had they been entirely successful in protecting themselves against insects, there would be fewer pest problems in agriculture (Fraenkel, 1959), but as we noted, domestication has often compromised natural defences.

Once a herbivore finds a potential food plant, there are those species on which it *will never* feed (*antixenosis*), maybe because that plant's defences against it are complete or because it lacks an essential nutrient. Then, on the range of plant species and varieties on which it *will* feed, suitability varies widely. For a given pest, this can be assessed in such innate attributes of the insect as growth rate, survival, achieve fecundity and, ultimately, its reproductive success (Section **10.1**), an ecologically meaningful bioassay of the plant's resistance. But is this effect due to plant defences, to nutritional inadequacy or both (Berenbaum, 1995)? That being said, good examples are the winter and gypsy moths' varying success on a variety of tree species (Sections **5.2.1.4(f)** and **5.2.1.4(g)**), and the graded performance of *Heliothis* on several cotton varieties, including those with high levels of gossypol, those lacking extra-floral nectaries and having 'Frego bract' (Maxwell and Jennings, 1980).

Plants often employ tannins and other phenolics that build up during the growing season, giving a quantitative effect and functioning against a wide range of insects (Feeny, 1970; Forkner *et al*., 2004). Tannins are a heterogeneous group of water-soluble, high molecular weight, phenolic polymers that can bind proteins. While some insects can reduce their effects, they may well have other important functions, as they are antioxidants and may protect plants from photodamage (Zucker, 1983; Close and McArthur, 2002, in Forkner *et al*., 2004). Cardenolides are found in many plants. They are often sequestered by insects and used for their own defences (Rothschild, 1972). But the plant's ability to build them depends upon water and nutrient supply, namely an external restraint. Further, when plants compete mutually they may be less able to defend themselves against herbivores and pathogens. The responses of plants to insects attacking or even ovipositing on them are far more complex than were imagined originally, a fine example of 'Goldberg's Lever' (Howe and Jander, 2008; see also Section **7.3.2.4(d)**).

Assuming that plants have evolved defence mechanisms because damage by herbivory reduces their fitness, we would further assume that this will bear a cost, although the scenario of a co-evolutionary arms race (Sections **2.4** and **8.2.1;** Moran and Hamilton, 1980; Jermy, 1984) is a further assumption. But if there are costs, are they general and significant (Mole, 1994)? Simms and Triplett (1994) found no fitness cost to the vine *Ipomoea* when attacked by the fungus *Colletrotrichum*. Bergelson and Purrington (1996), following Simms and Rausher (1987) in surveying the literature for evidence of cost, found it in <50% of cases. Trade-offs are not universal. As we noted, a plant might be unsuitable simply because it lacked some essential nutrient for an insect. Then, several of the studies purporting to show the induction of chemical defences are flawed statistically (Fowler and Lawton, 1985; Haukioja, 1990). Because of inadequate statistical replication, variation between individual plants was not factored out. We now know that for annual crop plants, the diversion of metabolites for protective purposes generally represents a minor drain on the photosynthetic machine, which normally provides more building blocks for growth than can be deployed (Foyer *et al.*, 2007). Rather like having more income than you can possibly spend, as Elton John once remarked to me. Also, there may be subsequent effects on the enemies of these herbivores (Price *et al.*, 1980; Wootton, 1994; Van Emden, 1999; Thaler, 2002; Ode, 2006). Additionally, we would expect that wild plants have evolved the least costly means of protecting themselves.

Because plants, and particularly trees, are modular organisms, there may be genetic variation between plant parts (Whitham and Slobodchikoff, 1981; see also Section **2.4.1**). It is also possible that insects can choose individual plants, or plant parts, that are poorly defended (Kessler and Baldwin, 2001), and/or more nutritious (Price, 1991), rather as mammalian carnivores often attack weaker prey. The former is certainly true for some bark beetles attacking conifers (Section **4.2.1.2(f)**). The cost would be relative, that is, if nitrogen was scarce, nitrogen-based defences would be relatively costly, and *vice versa*. Indeed, a plant's options are diverse. It may grow away rapidly from the attack, leading to a greater production of plant biomass, pass quickly through a vulnerable stage, or have storage organs free from attack (Herms and Mattson, 1992). Even so, the most obvious defences of plants are physical or chemical, and may well entail metabolic costs, although we expect apparent and non-apparent plants to differ. So highly apparent, long-lived trees should have the best defences. For example, some conifers have evolved diverse chemical defences of repellents and toxins that discourage all but the most specialized herbivores (Knerer and Atwood, 1973). Early successional species, such as lodgepole pine, do not defend themselves as well as climax species like grand fir (Raffa and Berryman, 1987). In my experience long-lived yew trees are rarely attacked, although sometimes eaten by vine weevils (Section **3.2.1.2(c)**) and galled by midges. Small plants and seedlings are the most vulnerable (Janzen, 1970; Lundberg and Astrom, 1990).

Chemical defences are more complex. To reiterate, there are *primary compounds* that take part in essential metabolic processes, are the main food required by herbivores, and do not differ greatly between plant species. Then there are *secondary compounds* that are not food for herbivores, may differ between plant species, and may protect them from attack. While the distinction between these compounds is not absolute, secondary compounds are usually derived from the plant's fundamental metabolism (Fraenkel, 1959; Jones, 1979; Blum, 1979). They are also found in fungi and microbes, specifically in those organisms lacking an immune system (Stamp, 2003b). These 'odd chemicals', as Fraenkel termed them, may be divided into four types. (i) There are a few inorganic ions such as selenium. For example, Brazil nuts contain relatively high levels of this element, presumably combating insect or fungal attack prior to germination. (ii) There are multiple organic compounds. Among these there are feeding deterrents that prevent insects from penetrating the plant. However, what may be a deterrent to most insects is often an attractant to a specialized few (Ehrlich and Raven, 1964; Rhoades, 1985; Rosenthal, 1986). For example, the mustard oils brassicas produce attract specialist aphids, flea beetles and pierid butterflies. But once an insect has penetrated the plant's tissues there are (iii) *pre-existing* (*constitutive*) and (iv) *induced* chemical defences (Haukioja 1980, 1990; Howe and Jander, 2008). The latter refers to the plant's ability to build defensive compounds and concentrate them at and around the attack site. Induction may be rapid or delayed. Optimal defence theory (Holland *et al.*, 2009) predicts that these systems compete mutually and that constitutive defences are used for high-value plant organs, such as mature fruits. Induced defences probably evolved since they drain the plant's resources *only when needed* (Karban and Myers, 1989). For example, some rice cultivars produce the ovicide benzyl benzoate only in response to oviposition by pest delphacid bugs (Section **13.3.2.2**). Bugs that tap the plant's vascular pathways can avoid toxic compounds stored in the parenchyma (Denno and Roderick, 1990). Also, plants may respond by translocating valuable nutrients away from the attack site, like a 'scorched earth' policy in warfare. Another way in which active plant defences differ (Kaloshian, 2004) is that some are *basal defences* that restrict enemy invasion, while others involve the *specific recognition* of the enemy by plant resistance (*R*) genes. This group of genes confers resistance to various enemies (insects, nematodes, microbes). They have a common structural component, the *leucine-rich repeat*, and their products share striking structural similarities.

The synthesis of induced defences is set in train by *elicitors*, substances of either plant or insect origin. Indeed, several plants distinguish elicitors in the saliva of insects from those resulting from mechanical damage to itself. Plant responses are often mediated through a ubiquitous class of chemical messengers called *jasmonates* (JA). Another response is via salicylic acid (SA; Stout *et al*., 2006), that reacts to attack by aphids and leaf miners, while ethylene (ET) is a further pathway. These pathways may act in concert (Kaloshian, 2004). When the plant responds to eggs laid upon it, the response may involve fluids and/or microbes on both eggs and the plant (Hilker and Meiners, 2006), constituting an early warning system. Plants also respond with volatiles to fluids deposited during oviposition. For example, when *Diprion pini* (Section **5.2.1.3(e)**) slashes *Pinus sylvestris* needles to lay eggs, the plant emits more terpenoid volatiles and less ethylene (Schroder *et al*., 2007).

Plants damaged by insects emit volatile compounds in greatly increased amounts (Vet and Dicke, 1992). They are often released preferentially during daytime, when they attract insectan enemies of these herbivores more effectively. They include terpenes, ethylene and the so-called 'green leaf volatiles' (Turlings *et al*., 1995; Takabayashi and Dicke, 1996; Kessler and Baldwin, 2001). Similar compounds, produced below ground (Rasmann *et al*., 2005; Rasmann and Turlings, 2008), attract entomopathogenic nematodes. Indeed, defensive compounds in general form an amazingly complex mixture: Poelman *et al*. (2009) identified 440 compounds within the crowns of attacked and control *Brassica oleracea* cultivars, although 'only 42 [of them] were present in all replicates'**!** This extreme complexity underlines the difficulty of experimental work on secondary compounds. But the plant has no further control over their use, and careful studies (Thaler, 2002; Rasmann and Turlings, 2008) show that they have great variation in attracting such enemies. For example, maize roots attacked by *Diabrotica* v. *virgifera* (Section **3.2.2.1(a)**) attract the nematodes *Heterorhabditis megidis* and *H. bacteriophora,* but not *Steinernema feltiae*. Specific blends of such compounds from maize infested by *Spodoptera littoralis* attract two braconid parasitoids, *Cotesia marginiventris* and *Microplitis rufiventris* (D'Alessandro *et al*., 2006). The former 'shows a keen ability for associative learning', namely to associate such blends with the presence of their hosts. What is truly amazing is that the volatiles may evoke adjacent plants into a state of biochemical readiness (Kost and Heil, 2006; Howe and Jander, 2008). Compounds used experimentally such as β-aminobutyric acid (BABA) can also enhance plant resistance to pests. This is related to the elevated expression of PR-1, PR-2 and PR-5 genes (Jakab *et al*., 2001, in Tiwari *et al*., 2013).

In terms of effects, there are *toxins* and *digestibility reducers* (Rhoades and Cates, 1976). Many toxins contain nitrogen, for example alkaloids, cyanogenic glycosides, glucosinolates, various proteins, peptides and non-protein amino acids. Others such as cardiac glycosides, saponins and quinones do not, and nor do several digestibility reducers: phenolics, tannins and various terpenoids. They should be less costly to produce, although the diverse polypeptides and small proteins that act as protease inhibitors do have nitrogen. The alkaloids include such memorable compounds as caffeine, nicotine, morphine, strychnine and cocaine. Symbiotic fungi also produce alkaloids (Clay, 1990). Glucosinolates and cyanogenic glycosides (a strong emetic for birds), which are stored by the plant, produce toxic breakdown products only during herbivory, the latter forming hydrogen cyanide. Defensive plant proteins include enzymes disrupting the insect's digestion and others attacking its peritrophic membrane (Howe and Jander, 2008), which protects the gut epithelium. There are also chemical mimics of insect pheromones and hormones. In balsam fir, a juvenile-hormone mimic (juvabione) in living tissue can interfere with the normal development of insects eating it. Other hormone mimics are found in the rhizomes of several ferns. In Kenya, even locusts avoid *Ajuga remota*. Experiments show that this plant has teratological effects on insect development (Rosenthal, 1986). Birch trees in Finland attacked by the geometrid moth *Epirrita autumnata* produce more phenolics (Haukioja, 1980). These inhibit digestion by trypsin in the caterpillars and increase their time to pupation. Severely attacked trees have elevated defences for several years, so the phenolics must be allocated to the leaves, or produced therein, several times. Even so, larval progeny from parents developing in high-density conditions are better at coping with these defences than those at low density (Haukioja and Neuvonen 1987, in Myers *et al*., 1998).

Karban (1987) suggested that such plant reactions, rather than age *per se*, are a general cause of the inferiority of plant food, but of course the build-up of enemies must also be accounted

(Section **12.3.2.1**). Phenolics appear to be 'rather stable end products' (Mattson, 1980b). Conifers produce several monoterpenes in response to attack by bark beetles, but this is costly (Raffa and Berryman, 1987). Like Bergelson and Purrington (1996), they point out that there may not be the often-expected trade-off between defence and reproduction. The most vigorous trees may simply grow the fastest, synthesize the highest levels of defensive chemicals and bear the most seeds. But another birch, *Betula resinifera*, in Alaska, uses a triterpene for defence, which requires >20% of its metabolic production. Again, up to 9% dw of *Plantago lanceolata* plants can be protective iridoid glycosides (Harvey *et al*., 2005), but these are exceptional cases. Naturally, defences operate only in the living parts of a tree; but the heartwood is extremely indigestible.

Some chemicals, such as tannins in oak leaves, build up during the growing season, providing universal protection (Feeny, 1970; Forkner *et al*., 2004), and may be typical of apparent, climax, *K*-selected vegetation. In contrast, hard-to-find non-apparent plants, which are often annual and *r*-selected, produce low concentrations of chemical deterrents that are effective against non-specific herbivores. Their specific herbivores, however, may not only detoxify these compounds, but also use their odour to detect this food (above). *Platyprepia* (Arctiidae) larvae can destroy or inactivate alkaloids in their guts (Karban *et al*., 2010).

While temperate, deciduous trees are in leaf for ~6 months, evergreens and conifers may retain leaves for 2 years, so we expect better defences. Although some tropical evergreens like *Cecropia* have a rapid turnover of leaves, which may be typical of gap phase species, others, like *Hernandia*, a climax species, retain them for 3 years (Garraway *et al*., 2008). But habitat structure may drive selection for the best defensive strategy (Price, T., 1997).

In Section **9.8** these strategies are considered as 'bottom-up' (q.v.) effects on herbivores, from a plant's perspective they are defences against the 'top-down' (q.v.) effects of herbivory (Section **10.1**). But there are limits, leaves with a thick cuticle cannot grow, while apart from metabolic cost, secondary chemicals are limited by autotoxicity (Southwood, 1988; Berenbaum, 1995). In those containing nitrogen, the availability of this element is also limiting (Lundberg and Astrom, 1990; White, 1993; Conner, 2003). As above, variation in the concentration of *primary compounds*, such as amino acids, sterols and vitamins, has an influence on the reproductive success of herbivores, and Berenbaum (1995) makes an eloquent case for this consequence. Whenever plant defences, from whatever cause, increase the period of juvenile development a *Williams' effect* may ensue (q.v.; Section **10.2.2.1**). In this context, I.S. Williams (1999), who fails to quote G.C. Williams' work, but in an otherwise extensive review of the literature, finds this effect occurs in about half the cases in juvenile endopterygotes, but not in the limited exopterygote data. Then predators, not parasitoids, are more likely to drive this effect. Probably some specialist herbivores and their parasitoids have evolved to a position in which they have negated the defences of their chosen plant food and often use them to their advantage (Harvey *et al*., 2005).

Plants, however, do show several compensatory mechanisms after damage, some passive and others active. For the former, peripheral defoliation leads to greater light penetration and then to greater productivity from more central leaves. Active mechanisms involve the re-allocation, rather than storage, of metabolites to repair damaged tissues. Damage often stimulates growth and reproduction (Paige and Whitham, 1987), but also causes delays. For reviews of plant defences see Blum (1979), Rhoades (1985), Haukioja (1990), Bernays and Chapman (1994), Berenbaum (1995), Karban and Baldwin (1997) and Howe and Jander (2008). For their diverse uses see Price *et al.* (1980), Barbosa *et al.* (1991), Ohgushi (2005), Ode (2006) and Karban *et al.* (2010).

2.5 Some Final Points

The ecological classification of plant pests given in Section **2.3** may be cross-classified with whether the pest is a biter or a sucker (see Fig. 1.2). Then, oligophagy and polyphagy can be a useful secondary level of classification. When it is helpful or necessary, insect taxonomy can be used as a final level, especially the basic division between Exopterygota and Endopterygota, and has many ecological consequences. Each pest is given its order and family in the heading. It is there both for reference and so that students will gradually become familiar with the insect classification by a process of passive absorption. Insects in their various orders are *very different from each other* in structure, physiology, ecology and behaviour, just as birds are from mammals.

As well as its current taxonomic classification, past or alternative scientific names (*synonymies*) for the pests may also be given, which can, for example, enable the reader to identify the pest in older texts. Each pest is also given a one-line description, rather like a newspaper headline. For example, *Aphis fabae* is described as 'A cosmopolitan pest and virus vector of legumes'. The brief description, while useful in providing the essential status of each pest, is qualified as necessary. Often a few additional, related pest species will be mentioned at the end of the main text. They may have *similar* ecologies to the major species considered.

The practical specifics used to control insect pests of crops by means of chemicals are not given here. Spraying insecticides, although necessary in some cases and often in emergencies, is increasingly regarded as, to borrow a phrase from statistics, a '*quick and dirty method*' (Section **13.2.3.1**). Also, the insecticides marketed often change every few years, so that specific recommendations would become dated, although there are a few treasured favourites such as malathion and diazinon. This book, being essentially ecological, emphasizes the integrated approach (Section **13.3**). The system of control used must be integrated with the pest's ecology, with the nature of the crop and with a view to minimize insecticidal residues both on the plant product and in the environment at large. But apart from using insecticides, this often involves sampling the pest's population by trapping. Insurance spraying must become a thing of the past. Cultural practices such as irrigation, ploughing, rolling, harrowing and modification of harvesting are appropriate, resistant varieties may be chosen (Section **13.2.4.2**), and planting times adjusted to combat pests. There is a further point. When economic entomologists speak of 'control' they do not mean the 'control' of insect numbers as used by population ecologists (Richards, 1961). Economic entomologists mean, 'kill it when it has reached, or is expected to reach, pest status', but population ecologists usually mean 'limitation below the carrying capacity (q.v.) by some natural means' (Section **12.3**). Diversity leads to confusion if we are not careful.

3 The Pests of Roots, Tubers and Sown Seed

3.1 General Introduction

Roots anchor the plant to the soil (Section **2.3.2.1**) and so assist stems, the axial part of the plant (Section **4.1**), in support. In trees and shrubs, they become woody rather like the stems of such plants. Fine roots absorb water and nutrients. Because the production of plant tissue below the ground is generally greater than that above it, unseen subterranean herbivory by insects, and also by nematodes, can have a considerable influence on plant tissue above ground (Brown and Gange, 1990; Masters *et al*., 1993) and on plant fitness. Root damage often causes symptoms similar to drought stress, but in turn to an increase in nutrients available to herbivores above ground (Masters *et al*., 1993, 2001). This can have outcomes for their populations and, in train, for those of their enemies. Both root and foliar feeding may influence the ecology of mycorrhizae and soil nematodes, interactions that are little researched. Not only are individual plants damaged, but also the species composition of biotopes may be altered. With moderate levels of grazing, densities of herbivores within the soil may even increase (Seastedt *et al*., 1988). Geographically, herbivores in the soil show considerable endemism in isolated habitats and landmasses (Hill, 1983; Brown and Gange, 1990).

Peripheral roots grow preferentially into localized regions where water and nutrients are concentrated (Jackson *et al*., 1990), the soil being notably heterogeneous (Sections **8.2.4** and **9.8**). They are frequently associated with fungal mycorrhizae. Within a restricted ambit they are downwardly mobile. Roots and underground stems may also be involved in asexual reproduction and the development of clones. Most importantly for our purposes, both roots themselves and specialized storage organs such as root and stem tubers, and in monocotyledons bulbs and corms, store the plant's metabolic resources. Thus, plants generally store resources within the soil where they are better protected. Indeed, subterranean plant organs represent a huge reservoir of biomass that is generally unavailable to herbivores above ground. Starch is the main medium of energy storage and comes in two forms, amylose and amylopectin, but sucrose too is often stored underground, sugar beet and sweet potatoes being obvious examples. Nitrogen for potential growth is stored as amino acids, particularly asparagine and glutamine. Recall that our hominoid ancestors, together with the pigs and peccaries, evolved to eat roots, tubers and bulbs as a major part of their diet. We are advised to eat a wide variety of plant food, a fact that attests to our need for a similar variety of plant storage compounds and metabolites. We should also follow the lead of many insects! But non-storage root tissues have much lower quality. Insectan root pests are mainly juveniles, using CO_2 emission (Guerenstein and Hildebrand, 2008) and root exudates to locate their food in the dark. While CO_2 provides a general cue, the latter are often specific to given plants, and as above ground, act as attractants, feeding stimulants or deterrents. While stores in these subterranean organs are rarely greatly depleted by insects insofar as the plant is concerned, when they affect marketable products, like potatoes and carrots, pest attack drastically reduces commercial value. Seedlings, however, are particularly vulnerable to damage at an early stage, especially during drought.

Soil insects, apart from predation by insectivorous mammals and carabid and staphylinid beetles, need mechanisms to avoid the ingress of entomopathogenic nematodes, such as *Heterorhabditis* and *Steinernema*. For example, a thick waxy cuticle protects wireworms and their spiracles have special plates to exclude these beasts (Eidt and Thurston, 1995), which are attracted to damaged roots (Rasmann *et al*., 2005). In contrast to insects above ground, parasitoids are of lesser importance in the soil (Hawkins and Lawton, 1987), although several genera of tachinid flies in the Dexiinae parasitize beetle

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larvae, *Bucentes* and *Crocuta* attack larval crane flies, and the peculiar wasp *Pelecinus* (Section **8.2.2.5**(**w**)) afflicts melolonthine larvae. But extreme physical factors can cause major mortality and soil insects often move downward to avoid drought and low temperature. Overall, moisture is the key physical factor for these insects since temperatures are buffered, particularly by increasing depth. Flooding can be catastrophic (see Section **10.2.3.4** for *Tipula*). For general accounts of insect herbivory below ground see Brown and Gange (1990) and Van der Putten *et al*. (2001).

3.2 Biting Pests

These root pests may be divided usefully into generalized feeders (e.g. wireworms, leatherjackets and cutworms) and specialized feeders (e.g. fiddler beetles, banana borers and carrot root flies). While the concept of *generalized* versus *specialized* often can be applied to other types of pest, it is most useful in the present case. Probably all biting root pests by their mechanical damage allow enhanced penetration of pathogens, which indeed some of them transmit. Grasslands under grazing are very vulnerable to these pests. Lightly attacked roots, however, may overcompensate with regrowth, and then greater uptake of minerals ensues.

3.2.1 Generalized or polyphagous feeders

Although there is normally a rapid turnover of living tissue (Stanton, 1988), particularly in the tropics, root systems often provide long-lasting food patches in which pest species can live and breed. These are in contrast to flowers, which are generally of short duration. Generalized feeders can switch from one type of crop to another, and often dead organic matter as well. They often switch either as different crops are planted in the same field in successive seasons (crop rotation, movement in time), or they can spread to adjacent or even to distant crops when plants or soil are transported (movement in space). Hence crop rotation is less effective than for specialized feeders, although some crops are more susceptible than others. The adults of different species have very variable powers of searching for new resources (Section **10.2.4.1**). These pests often feed on wild plants that may be related to the crops themselves (Section **13.1.2.2**). For example, generalized cereal pests often feed on wild grasses, which are also in the Gramineae. Some of these pests have an even wider range of food preference, for example wireworms feed on both living and dead plant material and, apart from field crops, often damage the roots of saplings of forest trees in nurseries. Even so, we should be sure that our generalized species are indeed good species, not a collection of cryptic ones (Section **1.3.4**).

3.2.1.1 Exopterygota

3.2.1.1(a) ORTHOPTERA; Gryllotalpidae. *Gryllotalpa*, *Scapteriscus*. Mole crickets. The family is small but generally distributed. Adults are relatively large (20–35 mm long; Fig. 3.1) and adapted for burrowing, as their common name indicates. The fore legs, with their various terminal plates, are equipped not only for digging but also for scything through rootlets. While most species are vegetarian, others such as *Scapteriscus acletus*, found in pastures, are mainly carnivorous (Forrest, 1986). Batches of up to 35 eggs are laid in an underground chamber. In many *Scapteriscus* spp. up to 450 eggs and ten batches may be laid, but oddly Forrest found no relationship of female size to either the number of egg batches laid or to egg size (Section **10.2.5.2**). But in *S. acletus* the number of eggs hatching per clutch and nymphal survival *are* related. Development through five instars takes 1 or 2 years, according to species and conditions.

Species of *Larra* (Sphecidae; Section **8.2.2.4**(**n**)) attack mole crickets (Malyshev, 1968), chasing them from their burrows. The sting affects only a temporary paralysis, during which they oviposit between the cricket's legs, resulting in the peculiarly grotesque situation of a parasitic larva feeding externally on an active host and, when larger,

Fig. 3.1. The mole cricket, *Gryllotalpa*. The plates on the front legs are used for scything small roots. Source: Wikimedia Commons, author Bernard Dupont.

circling it like a belt. Libersat *et al.* (2009) describe the host manipulation by such wasps. *Larra bicolor*, imported from lowland Bolivia, established a population in Florida in 1995. These active insects require plenty of nectar for energy and attempts in the 1940s to control mole crickets, using *L. americana* in the West Indies, may have failed because of an inadequate supply (Section **13.2.4.7**). *Ormia depleta* (Tachinidae) has been used to control these pests, and it too needs to feed on flowers. This fly employs an acoustic organ situated between its fore coxae to detect its male prey as they stridulate to attract females (Frank *et al.*, 1996). Nematode-entrapping fungi have been found growing on the cuticle of *S. borellii*, which may give them some protection from the endopathogenic nematode *Steinernema feltiae* (Section **13.2.4.5**). As in several other soil pests, ploughing or discing, especially after rain, destroys them, and poisoned baits are also effective.

3.2.1.2 Endopterygota

3.2.1.2(a) COLEOPTERA; Elateridae. *Agriotes lineatus*, *A. obscurus*, *A. sputator, A. mancus*. Wireworms. Cosmopolitan pests of roots, tubers and sown seed. Apart from the species above, there are many more in *Agriotes* itself and in *Athous*, *Corymbites*, *Ctenicera*, *Horistonotus*, *Hypolithus* and *Limonius*. These often have extensive distributions and probably broadly similar ecology. They comprise some 7000 described species (Hill, 1997). The larvae of *Agriotes, Athous* and *Ctenicera* are found abundantly in temperate pastures where they may reach densities approaching 20 million and a biomass of ~400 kg/ha, contributing to their being one of the most serious agricultural pests there.

In the UK, pastures tend to be more densely populated by *Agriotes* in the south-east and less so in the north-west, a feature that may relate to temperature and rainfall differences (Section **12.3.4.1**). The larvae are up to 40 mm long and look like bits of yellow, insulated electrical wire. They burrow more deeply in dry summers and in cold weather and may enter diapause if it is cold enough. They take 3 to 5 years to complete development, less in southern areas and longer in northern ones. In pasture they feed on grass roots, homing in on root exudates such as asparagine and aspartic acid. Although they may tunnel into roots, they do not ingest bulk plant material but imbibe fluids from their food (Eidt and Thurston, 1995). Feeding causes little obvious damage in pasture, but this is because the grass plants compete intensely for space, thus filling up any gaps. But as with frit flies (Section **4.4.1.1(g)**), it allows non-preferred plant species to increase. *Agriotes* feeds more actively in damp weather, especially in spring and autumn. In drought conditions, feeding is slower, but wireworms may penetrate tubers at this time, or even fruits such as tomatoes if they touch the ground. Conversely, flooding eventually kills most wireworms. They are also adversely affected by acidic conditions, and *Limonius* wireworms, which are pests of sugar beet in the USA, are characteristic of alkaline soils. Adults of temperate species normally emerge in autumn but reside in their pupal cells until spring, when the eggs are laid. The adults of most species fly only at relatively high temperatures, slowly and not far. Females typically select pasture for oviposition and the eggs hatch in 2 to 4 weeks. Wireworms also commonly occur in forest soils (Penev, 1992) where, like crane fly larvae (Freeman, 1967b), they are an important element in the soil macrofauna (Section **8.2.4**).

Old pastures normally have dense wireworm populations. When ploughed up to plant cereals or root crops such as beet, mangolds, potatoes and carrots, these suffer attack, with larger larvae doing the bulk of the damage. Strawberries are also susceptible but can be partially protected by intercropping with wheat planted a week or so earlier. The most resistant crops are barley, kale, rape, peas and beans. Wireworms also destroy tomato and cotton roots and brassica seedlings. Partial damage may cause premature flowering and hence crop losses. Autumn ploughing kills few wireworms as their integument is tough, although it exposes them to avian predation and destroys pupae and adults in their cells. But their physical toughness and the fact that they are long lived means that considerable numbers will be present in a subsequent year to infest the new crops. Since they fly weakly, however, appropriate crop rotation can suppress them. In the past, aldrin and other chlorinated hydrocarbons such as benzene hexachloride (BHC) have been used often as a soil treatment, but these are now banned in most countries owing to their extreme persistence and bad environmental effects (Section **13.2.3.2**). Compacting the soil with rollers often reduces wireworm attack as it limits their mobility. In low-lying areas, flooding has been used to suppress them, but such inundation requires some 6 weeks for effective control and may have various ill effects on the soil. In the USA, by contrast, withholding irrigation from drought-hardy lucerne crops also kills wireworms. As with most soil insects, however, little is known of their natural mortality, although carabid and staphylinid beetles prey on them. Entomopathogenic nematodes such as *Steinernema* and *Heterorhabditis* carry various *Xenorhabdus* bacteria commonly present in the soil (Kaya and Gaugler, 1993). But wireworms have a thick cuticle and special spiracular plates, which resist their entry (Eidt and Thurston, 1995). Because of their long life in the soil such defences would seem imperative. When these nematodes penetrate insects their symbionts escape and kill the host rapidly, with the nematodes feeding on the insect's degenerating tissues and the bacterial colony.

Spring cereals are protected by prior chemical treatments to the seeds, but this does little to reduce wireworm numbers, since after ploughing pasture there is an abundance of buried dead grass on which they feed (Vernon *et al*., 2003). In mid-western USA, maize seed may be almost totally destroyed after being sown in ploughed pasture. Potato tubers, which they have bored, are particularly susceptible to bacterial rot during storage, caused by the Gram-negative bacilli *Erwinia* spp. This damage produces a '*multiplicative effect*', meaning that much more plant tissue is ultimately destroyed by the pathogen than is consumed by the insect. This effect is typical of what may occur in infected plant products in storage, as diverse as tubers (sweet potatoes, various yams), onions, top fruits (apples, pears, mangoes) and grain, and we will refer to it again. Other elaterid genera include the pan-tropical, polyphagous *Lacon*, and *Conoderus* and *Melanotus*, which attack sugar cane. 'False wireworms', *Eleodes* and *Blapstinus* (Tenebrionidae; Section **6.3.1.2(l)**), occasionally damage sprouting seeds.

3.2.1.2(b) COLEOPTERA; Scarabaeidae. *Melolontha*, *Phyllopertha* (= *Anomala*), *Popillia*, *Dermolepida*. Chafers and related beetles. Mainly temperate pests of roots as larvae, with polyphagous adults. These are big, fat, white and ugly C-shaped larvae found in the soil (Fig. 3.2). Depending on species and location they may spend more than a year in this stage. Like wireworms they move down in the soil in cold or dry weather. The pattern of attack in these beetles is that larger larvae are phytodetrivores but eat plant roots as a supplement, especially during drought, and hence become pests. Prior to and often during egg laying the adults feed on leaves, particularly those of trees and shrubs. They are less often pests at this stage.

Fig. 3.2. A mature larva of *Melolontha*, a pest of plant roots. Note the lack of pigment. Source: Wikimedia Commons, author Falko Zurell.

The European *Melolontha melolontha* is up to 40 mm long. Its unusual reproductive behaviour gives us an insight into the way it causes damage. Newly emerged adults leave their natal fields and fly to the nearest woodland. They navigate by scanning the locality for irregularities that stick up from the horizon, but also use heliotaxis (Prokopy and Owens, 1983; Section **10.2.4.4**). In woodlands they eat various fresh leaves and developing fruits, mate and, when their ovaries have matured, females make a 'bee-line', or better, a 'chafer-line', for a field. Swarming males find their mates using the leaf volatiles released during feeding (Reinecke *et al*., 2006). Batches of ~20 eggs are deposited ~10 cm deep in field soil. Several egg batches, according to the length of a female's survival and probably her size, are laid in this to-and-fro behaviour.

Chafer grubs remain in the larval stage for up to 3 years, diapausing in winter, so, as in wireworms there is a carryover of the same individuals from year to year in the same field. They are often pests in sports turf, especially golf greens. The damage caused by a single large grub may amount to as much as a divot from a driver. In addition, the larvae attack a variety of field crops and in this case repeated discing or heavy rolling will reduce their numbers significantly as they are soft and squashy, but is more effective in mild weather when they are near the surface. Because of the female's shuttling behaviour, field strawberries are vulnerable when planted near woodlands. Like wireworms, they also attack the roots of trees. In France, adults may be minor pests of fruit trees, since they consume the leaves and scar young apples, pears and plums. Larval *M. hippocastani* are similar pests in forest nurseries. In Switzerland, they have been controlled by the *sterile male technique* (Section **13.2.2.1**), while in Germany various mixtures of leaf volatiles and specific sex hormones have been used to trap males (Reinecke *et al*., 2006). *Hoplia philanthus* and *Serica brunnea* are similar pests thriving in grassy orchards. The small garden chafer, *Phyllopertha horticola,* has an annual life cycle. It is more frequent in light, porous soils and may attack crops planted after grassland is ploughed up. Females emerging from the sward are quickly mated and return to the soil to oviposit. As with the effects of some other root-feeding beetles, drought stress of the plants may result.

In North America, the common genus *Phyllophaga* (= *Lachnosterna*) contains many species. The greatest damage their larvae cause is often when pasture is ploughed and maize is planted, but *P. crinita* can be damaging to short-grass prairie in Texas, where larval densities may reach ~50/m^2. Several species have 3-year cycles of numbers corresponding to their time for development (Davidson and Lyon, 1986). It would be instructive to investigate this regularity: there may be a like relationship to that in the cycles of the moth *Xestia* (Varkonyi *et al*., 2002; Section **5.2.1.4(g)**), which are probably driven by a parasitoid with an annual life cycle. Indeed, *P. anxia* larvae are parasitized by the peculiar wasp *Pelecinus polyturator* (Section **8.2.2.5(w)**), which employs its odd, elongated abdomen to reach them (Lim *et al*., 1980; Borror *et al*., 1989).

Fig. 3.3. The adult of *Popillia japonica*. The metallic green colour is an adaptation to reduce the speed of over-heating in sunshine. Source: Wikimedia Commons, author Robert Webster.

Popillia japonica, the Japanese beetle (Fig. 3.3), whose larvae attack golf courses and parkland sward in North America, is a similar pest. The metallic green and bronze adults are ~1 cm long. They are highly polyphagous and consume the aerial parts of several hundred species of both dicotyledons and monocotyledons. Like cockchafers, they cause damage to the leaves of top fruits, but also attack ornamentals and some vegetables (Potter and Held, 2002). In a wide survey of Ohio, USA, Polivka (1960) found population densities of these grubs to be inversely related to pH. Indeed, females prefer to oviposit in acid soils (Davidson and Lyon, 1986). But adding alkaline material (lime, dolomite) to the soil had no effect on larval survival (Vittum, 1984). The larvae, however, do require temperatures >20°C. The beetle was foolishly introduced into New Jersey about 1916 from eastern Asia, and, despite early efforts to contain it, now affects most states east of the Mississippi and those in eastern Canada. Its success may well be associated with the increasing cultivation of greensward.

Females lay a few batches of 10–25 eggs in the soil, feeding between batches, rather in the manner of *Melolontha*. Batch size is particularly affected by the quality of the diet (Section **10.2.5.2**). The life cycle is annual in the south and biennial in the north of its distribution, where second or third larval instars enter winter diapause. They move deeper in the soil in cold weather and may resist up to −7°C. In the 1930s, the endopathogenic nematode *Steinernema glaseri* was applied with mixed success as a biocontrol agent (Kaya and Gaugler, 1993). *Bacillus popillae* may control this beetle and might be effective against other coleopteran pests in the soil. Another European chafer causing damage to turf in north-eastern USA is *Amphimallon* (= *Rhizotrogus*) *majalis,* whose adults are short lived. *Cyclocephala borealis* and *Macrodactylus subspinosus* (rose chafers) are also pests. The polyphagous *Maladera matrida*, described in Israel (Harari *et al*., 1994), forms mating aggregations that apparently result from their attraction to plant volatiles from chewed foliage.

The indigenous scarabaeid beetle, *Dermolepida albohirtum*, affects cane-growing regions of Queensland. It is the most damaging pest of Australian sugar cane (Sallam, 2011), causing annual losses often >AUS$10 million and ~AUS$40 million in outbreaks, with densities exceeding 150,000/ha. These occur in wet conditions. Larval damage to cane roots occurs in late summer and autumn, and tends to be greater if soils are deficient in organic matter. Symptoms include yellowing of the leaves and lodging. Adults usually emerge in spring (October to December), but later if there are drought conditions. Again, as in *Melolontha*, they initially aggregate, mate and feed on the leaves of trees before flying to the fields to oviposit. As in *Tipula paludosa* (Section **3.2.1.2(f)**), drought at the time of reproduction may reduce fecundity and larval survival. Mature larvae dig deeply into the sub-soil prior to pupation often reaching a depth of 60 cm. In drought there is high attrition of more superficial pupae, while adults are less active and so easily desiccated. Larval diseases are caused by the protist *Adelina* spp., by the bacterium *Paenibacillus popilliae* and by the widespread fungus *Metarhizium anisopliae*. *Adelina* may act as a density-dependent pathogen but is susceptible to dry conditions (Sallam, 2011). Predators include birds (e.g. *Ibis molucca* and *Carphibis spinicollis*), bandicoots, frogs and flying foxes, and the larvae of the giant elaterid beetle *Agrypnus mastersi* and of the asilid fly *Promachus doddi*. Two fossorial scoliid wasps (Section **8.2.2.5(y)**), *Campsomeris* spp., paralyse and then oviposit on the larvae.

Other Australian cane scarabs are *Antitrogus consanguineus*, *A. parvulus*, *Lepidota crinita* and *L. negatoria*. These beetles were formerly suppressed with organochlorines. When these were withdrawn in the late 1980s, the beetles resurged (Horsfield *et al*., 2008), but slow-release formulations of chlorpyrifos are often effective and entomopathogenic nematodes have been used (Arthurs *et al*., 2004). *Heteronychus* spp. affect sugar cane at ground level in Africa and Australasia, while *Holotrichia* spp. are polyphagous Eurasian chafers. *Holotrichia serrata*, *H. consanguinea* and *H. reynaudia* are important pests of groundnuts in several Indian states (Anitha *et al*., 2005), while other *Holotrichia* spp. are pests in Korea. *Holotrichia serrata* and *Heteronyx piceus* also affect this crop in Queensland (Rogers *et al*., 2005).

3.2.1.2(c) COLEOPTERA; Curculionidae. *Otiorhynchus* (= *Brachyrhinus*) *sulcatus*. Vine or black vine weevils. Flightless, parthenogenetic, horticultural pests of several temperate crops, shrubs and young trees. Weevils form an immense group dating from the Jurassic (Farrell, 1998). This beast reproduces by the unusual method of thelytokous parthenogenesis, namely females lay unfertilized eggs that develop into a clone of daughters identical to, or very similar to, their mother. Even so, parent–offspring conflict (Trivers, 1974) may exist (Clark *et al*., 2011). For example, even a single weevil can initiate attacks (Son and Lewis, 2005) that are often localized and severe. This species has a disjunctive distribution, affecting parts of temperate Europe, Japan, southern Australia, New Zealand and the Americas. Adults have a life expectancy of several months, one inversely related to temperature above ~10°C. In the laboratory when fed a *Rhododendron* cultivar, both achieved fecundity (AF; ~1100) and viability of the eggs (~90%) peak at 21°C. At 15°C and 26°C, AF is about half and viability is also reduced (Son and Lewis, 2005). The type of adult food influences the time for adult maturation, longevity and fecundity (Nielsen and Dunlap, 1981). Field AF is ~500. On raspberry, different cultivars result in changes in AF and survival, but no link exists between female preference and larval performance (Section **10.2.3.8**; Clark *et al*., 2012). The pest is univoltine, overwintering mainly as larvae in cooler regions but also as adults in warmer ones. The lethal dose that kills 90% (LD_{90}) of overwintering larvae (Section **10.2.3.2**) is –6°C and 9 days.

The nocturnal adults on leaves and larvae on roots are highly polyphagous (Masaki *et al*., 1984; Moorhouse *et al*., 1992; Clark *et al*., 2011). Adults eat characteristic notches from the leaf margin, a useful proxy for the presence of larvae in the soil. Over 150 species, both monocotyledons and dicotyledons, are potential food plants. These weevils develop well on members of the Rosaceae, but vines, rhododendrons, black currants and cranberries are also attacked, and cyclamen is very susceptible. For some plants, larval attack at the base of the stem is the most damaging. Adult defoliation of vines, which they can ring bark, is often more critical than larval damage. With such extensive polyphagy, wild, reservoir populations (Section **13.1.2.2**) are always present.

These weevils are prey to rodents and insectivorous mammals, with hedgehogs being very fond of them. Toads, starlings and poultry consume them avidly. Carabid beetles, ants and earwigs eat the juveniles. The fungi *Metarhizium anisopliae* and *Beauveria bassiana* often attack them and may be used to control them, and entomopathogenic nematodes have been used (Arthurs *et al*., 2004; Section **13.2.4.5**). Any insecticidal control should target the larvae and/or pre-reproductive adults, the organophosphates fonofos and chlorpyrifos (Section **13.2.3.2**) being effective for the former.

Related species include *O. ovatus*, *O. clavipes*, *O. raucus*, *O. rugostriatus* and *O. rugifrons*, which also attack strawberries and other crop plants. *Otiorhynchus cribricollis* is found in the Mediterranean region and attacks olives, grapes and figs. These weevils have a tendency for parthenogenesis. The adults may live for more than 1 year and are polyphagous on various leaves. Several other genera of these 'short-snout' or adelognathine weevils exist, some being more important for their larval damage to roots and others for their adult damage to foliage. In drier parts of Central and Eastern Europe and Iran, *Bothynoderes punctiventris* can be a devastating weevil on sugar beet, eating into the developing tap root. Other genera include *Sitona*, *Exophthalmus*, *Peritelus* and *Phyllobius*. The oligophagous species are considered in Section **3.2.2.1(b)**.

3.2.1.2(d) LEPIDOPTERA; Hepialidae. *Hepialus* spp. Swift moths. Mainly temperate pests of roots. Hepialid moths are structurally primitive. Adults have rudimentary mandibles and similar venation in fore- and hindwings, which are operationally linked by a unique lobe, the jugum. Their genitalia have classificatory value, and are quite different from those of other moths. Indeed, these moths have an anatomy unlike that of most Lepidoptera, with ancestors going back over 160 million years ago (Ma). Their life cycle may last 1 or 2 years depending on conditions. *Hepialus humuli*, the ghost swift, and *H. lupulinus*, the garden swift, are essentially pests of grasslands and attack a variety of agricultural and horticultural crops (Alford, 2007), including various cereals, legumes, potatoes, parsnips, carrots, swedes and strawberries. As with wireworms (Section **3.2.1.2(a)**), crops are more vulnerable when planted after ley. Some species, including *H. humuli*, also bore into woody roots. They are truly generalized pests and their gross ecology is comparable with *Tipula* (Section **3.2.1.2(f)**), although they are in a different order. Both pests have ephemeral, non-feeding adults, while the males of some species form mating swarms at dusk. *Hepialus humuli* is sexually dimorphic, with males having glossy white wings while in the females they are a sandy colour. Again, the long-lived larvae inhabit the soil. Males of some species are unusual in that they produce, from tibial scent glands, pheromones attractive to conspecific females (Schultz *et al*., 1990). These compounds belong to a class of volatiles unknown in other insects.

On summer nights fecund females flutter above potential larval feeding sites, scattering up to 800 eggs aerially. The maximum potential fecundity of the Australian swift moth *Abantiades magnificus* is >10,000, making it one of the most fecund of all insects. Like *H. humuli* its larvae eat roots, in this case those of eucalyptus. In India, *Sahyadrassus malabaricus* larvae bore a variety of sapling trees including those of teak, *Tectona grandis* (Nair, 2007). The adults rest in a pendulous manner, resembling dead leaves. Swift moth larvae usually make tunnels in the soil lined with silk. Silk production in larval moths is a common feature and influences their ecology in several ways, as we shall see. In temperate species larvae continue to feed during winter at a rate depending on the mildness of the prevailing weather. Cultivation of the soil reduces their numbers as they are relatively soft bodied and easily injured. *Oncopera fasciculata* larvae may attack pastures in South Australia, but easily drown in soils that become waterlogged. They may survive flooding, however, if tussocky grasses are available as refuges (Andrewartha and Birch, 1954). In western USA, *H. californicus* feeds on roots of the perennial lupin, *Lupinus arboreus*.

3.2.1.2(e) LEPIDOPTERA; Noctuidae (>22,000 spp.). *Agrotis segetum, A. ipsilon, A. exclamationis, Actebia fennica, Amathes* and *Apamea* spp., *Crymodes devestator, Euxoa nigricans, Feltia subterranea, Loxagrotis albicosta, Mythimna* and *Nephelodes* spp., *Peridroma, Porosagrotis orthogonia, Proxenus* and *Spaelotis* spp., *Autographa gamma, Triphaena pronuba*, *Xylomyges curialis*. Cutworms. Cosmopolitan pests of seedlings, roots, tubers and underground stems. Cutworms are the larvae of several noctuid moths, commonly of those given above. While this list is extensive it is far from exhaustive. They are, hence, of comparable diversity to wireworms and belong to a large family of stout, medium-sized moths, which are structurally more advanced (q.v.) than the Hepialidae. They share many characteristics with armyworms and *Heliothis* spp. (Section **6.2.1.2(h)**). Late larval cutworms attack diverse seedling and young plants, but are especially damaging to young brassicas and carrots. From 1917 to 1922 an outbreak of *Porosagrotis* in the

USA, from Montana to Colorado (Cook, 1924), affected extensive areas of wheat, causing up to 45% destruction of the area seeded. To the north of this region both winter and spring wheat are grown, the former surviving well under a good snow cover and the latter being used as cattle fodder if the summer is poor. Occasionally, like *Peridroma saucia* and *Nephelodes minians* in the USA, *Porosagrotis* becomes important on lawns and sports turf, while *Xylomyges* attacks citrus. Unlike the soil pests discussed above, cutworms develop rapidly, particularly so in the tropics, while even in temperate regions the life cycle may be completed within 6 weeks under favourable conditions. In northern regions some species overwinter as larvae in the soil and are especially destructive to early sown vegetables. According to species and location there may be from one to four generations per year even in temperate regions. This speed of development and the advanced powers of searching that the adult females possess, make them difficult to control, especially as some species also have a high AF.

Many of these moths, in common with related *Heliothis* spp. and armyworm moths, are highly migratory, often moving in low-level jets at the top of the nocturnal temperature inversion (Section **10.2.4.5**). In Europe, *Autographa gamma* arrives in northern regions in summer from the Mediterranean, and has a reverse migration in autumn. In North America, *Agrotis ipsilon* and *Peridroma saucia* can fly several 1000 km by this means (Burt and Pedgley, 1997). After migration, females are often attracted to slicks of water vapour from irrigated fields. Having found a humid slick they turn upwind, a behaviour eventually bringing them to the source. They may also detect plant volatiles. These attacks are a recurrent problem with irrigated crops in arid areas. They lay numerous eggs on the soil. The young larvae locate the plant by chemosensory means, being attracted to root exudates. The name 'cutworm' is derived from the infuriating habit of the large larvae of cutting down several young plants at soil level in a single night. They run down a row and, like a fox in a fowl pen, destroy much more than they can eat. Cutworms are one of the main scourges of cash crops on Caribbean islands.

Several ichneumons (*Campoletis intermedius*, *Hyposoter exiguae*, *Nepiera marginata*), braconid wasps (*Meteorus vulgaris*, *Microplitis feltiae*) and tachinid flies (*Linneamyia* (= *Bonnetia*) *comta*, *Eucelatoria armigera* and *Gonia capitata*) parasitize cutworms. They also fall prey to carabid and staphylinid beetles.

All of these generalized pests attack a multiplicity of crops and other plants. Their populations are maintained by a variety of wild plants as well as by cultivated ones (Section **13.1.2.2**). Hence, it is possible to kill them only on a local scale – in fact, only on the crop presently under cultivation. So growers must check regularly for infestations. In most cases roots are damaged and then the symptoms of attack, wilting and yellowing of the aerial part of the plant become visible, especially under drought conditions. Because these insects inhabit a large volume of soil, insecticidal treatments tend to be expensive, as commensurately large amounts of chemicals are needed. When using such a treatment the porosity of the soil is an important factor in its efficiency. A friable soil allows rapid penetration to depth, while clays prevent it. Clay minerals also adsorb insecticides, as do decomposing organic materials. In some species the young larvae are drowned under saturating irrigation. As with leatherjackets (Section **3.2.1.2(f)**), some measure of control can be obtained by using poisoned baits. More recently, entomopathogenic nematodes have been used against them (Arthurs *et al*., 2004; Section **13.2.4.5**).

HIGHLIGHTED PEST

3.2.1.2(f) DIPTERA; NEMATOCERA; Tipulidae. *Tipula paludosa*. Leatherjackets. Pests of roots in temperate Europe, more recently in North America. Pest leatherjackets are usually the soil-dwelling larvae of the common crane fly *T. paludosa,* although a few other species, such as *T. oleracea*, *T. vernalis*, *Nephrotoma quadrifaria* and *N. flavescens*, have been implicated on occasion. The life cycle of *T. paludosa*, a large and sometimes abundant fly, often descriptively called 'daddy-long-legs', is annual, while that of the closely related *T. oleracea* is bivoltine (Freeman, 1968; Blackshaw, 1988). In Europe, adults of both species emerge in late August and September, but *T. oleracea* has another emergence in May and June in southern England (Freeman, 1968; Freeman and Adams, 1972). The exarate pupae are sufficiently mobile to break through to the soil surface, being 'pharate adults' enclosed in a pupal sheath, their wings yet to expand (Hinton, 1946). Their mobility is due to the adult wriggling inside the pupal case, which has backwardly directed spines. They emerge shortly before darkness.

As males emerge first in the season, the sex ratio is initially male biased but then becomes female biased. The searching males, who fly in numbers low down over the dewy turf, quickly mate with the teneral females.

Mated females are so heavy with eggs, up to 650/female, that they cannot fly, even though their exoskeleton has hardened. They begin to oviposit where they emerge without selecting an oviposition site except on a small scale. They simply lay eggs where they have developed, there being no dispersive flight. Eggs are shiny black and have a filament that tends to anchor them. Females may be seen jabbing their ovipositors into the soil to deposit single eggs, often unloading the majority during their first night. Having done so they become flight-worthy and now deposit eggs in places distant from the natal site, the reverse order of operations from that in most insects (Johnson, 1960, 1969; Dingle, 1972, 1996), which disperse or migrate *before* they lay eggs and is termed the *oogenesis-flight syndrome* (Section **10.2.4.1**). In another grassland species, *T. pagana*, which emerges in late October, the females are *brachypterous*.

Crane flies have short adult lives: they imbibe water but rarely feed (Pritchard, 1983). Mark/recapture studies (Freeman, 1964) give rates of adult survival of ~70%/day in *T. luna* and even less in *T. subcunctus* (= *czizeki*), which is related to *T. paludosa*. At such a low rate a cohort of 100 adults emerging on a given day would reduce to only eight at the end of a week. Low rates are also recorded for other Nematocera such as mosquitoes (Section **7.3.2.1(b)**) and non-feeding Cyclorrhapha such as bot flies (Section **7.4.1.1**).

The eggs of these *Tipula* absorb soil water and hatch in ~2 weeks if not stressed by drought (Meats, personal communication, 1966). First larval instars are very vulnerable to desiccation, so that in a dry autumn their numbers fall dramatically. Milne *et al.* (1965) show that leatherjacket densities in north-east England are related to the amount of rainfall in the period when the eggs are being laid and the larvae are small. In British Columbia and Washington State, the characteristic autumn rains could be a reason for *T. paludosa* recently becoming a pest there. Survivors reach the third larval instar by November and densities may be >3 million/ha in grassland. But in spring, when they are rapidly growing fourth instars at densities >1 million/ha, they may damage plants. For spring barley, the economic injury level (Section **13.1.1**) is 280,000/ha (Blackshaw, 1988). In clover/rye grass sward, the legume is more affected than the grass. This is a specific example of a general effect (Brown and Gange, 1990). As we noted earlier, herbivory below ground may influence floral composition above it.

Enlightened farmers will be aware that heavy damage to crops is likely to occur if the preceding autumn has been wet, especially if adults have been seen in abundance, a situation where, with even slight ecological knowledge, a future pest attack may be predicted with some confidence. To get a better assessment, crane flies can be caught in field traps. Green basins containing water with a little detergent work well, but as expected catch males preferentially (Blackshaw, 1987). Crop rotation is effective as emerging females lay the bulk of their eggs where they emerge. Chlorpyrifos will kill them, but since larvae leave their burrows to forage on damp nights, they are attracted by poisoned baits and their numbers thereby reduced. Pasture may need a nitrogenous fertilizer to recover from their depredations. Because they are distributed near to the soil surface, they are vulnerable to tillage that destroys them mechanically or exposes them to avian predation. Blackshaw (1988) found that ploughing plus rotavating reduced their density by ~70%. It is a common sight in autumn to see gulls following the plough to feed on various insects as they surface. On Anglesey in north Wales, where there are extensive pastures and heavy rainfall, huge populations of *T. paludosa* emerge on September evenings, and flocks of gulls may be seen consuming them avidly.

The larvae of most crane fly species feed on decomposing material in the soil, which they shovel into their guts with spatulate mandibles. But in the final instar, both *T. paludosa* and *T. oleracea* larvae have relatively large mandibles and devour living plant tissue (see Fig. 5 in Freeman, 1967b). Maybe this is the reason why they can be serious pests while other, numerous *Tipula* species are not. Even *T. oleracea* can damage barley following a rape crop (Blackshaw, 1988). Attack is usually evident under drought conditions in early summer, either because more living plant tissue is eaten, and/or because plants can withstand less damage. Where winter wheat follows ley, ploughing should be done in August, so destroying the frail pupae and reducing subsequent oviposition. Considerable often unnoticed damage occurs to permanent pasture. In wet years, fields that would normally be too dry to support *T. paludosa* become colonized by female migrants, the *carrying capacity of the landscape* being greatly increased (Sections **6.3.1.1(c)**, **11.1.2** and **12.3.4.4**). This results in a larger area of crops affected and more economic loss. But a summer drought and a dry September can kill the larvae (Milne *et al*., 1965), drastically reducing the number and area of favourable habitats, resulting in population crashes on a landscape scale, a similar dynamic to that of many mosquitoes from temporary habitats (Section **7.3.2.4(c)**).

Tipula paludosa larvae contain a variety of internal, microbial commensals and parasites. The former is probably involved in digestion as cellulolytic capacity is known in the Tipulidae (Martin, 1991). The latter causes various levels of disease. Both Tipula *iridescent virus* and Tipula *nuclear polyhedrosis virus* are often found at low levels (Carter, 1976), but since dead larvae disappear one is unsure of the mortality they cause (Section **13.4.2**). Lethal bacilli are also found. Various gregarines and coccidia are common but appear to do little harm. The former, however, is thought to retard development further when their hosts are short of food as in some crickets, locusts and beetles (Zuk, 1987). The generally lethal tachinid flies *Bucentes* spp. (= *Siphona*) have been reported. *Tricoparia* and *Crocuta* are also known from *Tipula* spp. Carter records the phorid fly *Megaselia paludosa* from *T. paludosa*, noting that the latter survived the attack. Non-lethal parasitism probably causes reduced AF (Section **10.2.5.6**). *Tipula paludosa* larvae attack and probably kill and consume one another in the field. In the laboratory at densities representing 6 million/ha, such mortality was estimated at ~3%/day (Freeman, 1967b). Survivors develop black scars of the event. Similar scars are found under field conditions, although predatory beetles may also cause them. Such cannibalism is also known in *Dolichopeza* crane flies (Byers, 1961). It seems that most intraspecific aggression is dependent on population density, providing a brake on increase (Section **10.2.3.7**). But note that the physical factor of autumn drought may so reduce density, so that in the following spring competition (Section **9.8**) for space becomes insignificant (Section **10.1**).

The less numerous *T. oleracea* and *T. subcunctus* are very similar to *T. paludosa* as adults, excepting that their females are long-winged and can fly full of eggs. In the south-west USA, including Texas and California, *T. simplex* may destroy rangeland grasses (Hartman and Hynes, 1977), reaching densities of 3000/m^2. The eggs are deposited in a batch of ~100, often in a cattle hoof print, these beasts operating as *ecosystem engineers* (Section **10.1**). In addition, the larvae aggregate under their faecal pats. *Tipula acuta* is also found in this region. In the UK, *T. vernalis* often damages fine grasses used on golfing greens. The aquatic larvae of *T. lateralis* can live in watercress beds but prefer dead to living leaves. The yellow crane flies *Nephrotoma flavescens* and *N. maculata* have been implicated, on occasion, as pests of cultivated grasses.

3.2.1.2(g) DIPTERA; CYCLORRHAPHA; Muscidae; Anthomyiinae. *Delia platura, D. florilega*, *D. antiqua*. Bean seed flies or corn seed maggots, and onion flies. Temperate pests of sown seed. These *Delia* spp. are all ecologically similar, and more grossly so to wireworms, in that all have large, widespread larval populations subsisting on decaying organic matter within the soil. But they infest sown seeds when these are infected with pathogens, later destroying them and the seedlings. They are common in the UK on leeks, seedling bulbs and salad onions (Ellis and Scatcherd, 2007). *Delia antiqua* remains a widespread pest in North America (Werling *et al*., 2006). It shows high levels of attack along field margins and near woodlands in New York State, where it is trivoltine. Adult populations can be estimated with water traps painted white.

Unlike wireworms, however, their life cycle is short – a matter of weeks according to prevailing temperature – and their adults are more mobile. The shortness of an insect's life cycle is the main factor in promoting a high rate of increase of population numbers (Section **11.5.2**). Adult flies emerge from pupae in the soil in spring and females each lay 200–300 eggs in the soil surface. Female *D. antiqua* show crepuscular activity (McKinlay, 1992). The larvae attack sown seed of all types. They may be destroyed if not dressed and sprouting seeds are damaged, resulting in distortion. Warm, fertile soil promotes rapid germination and reduces damage because the larvae have less time to do their dirty work, whereas when the soil is cold or infertile the damage is greater. Where grain is 'over-sown', that is, more seed is drilled in than can possibly achieve maturity, their effect is generally small. This recalls the rustic Hertfordshire rhyme:

> Three seeds to sow,
> One for the crow,
> One to die and one to grow…

Indeed, cereals, sugar cane and cotton show great tolerance to early damage because of regrowth or reduced competition (for light and nutrients) from adjacent crop plants (Matthews, 1994). Damage to onions, however, can be considerable, extending into larger bulbs. The insect growth regulator (Section **13.2.3.2**) cyromazine, applied as a seed dressing to onions, is a useful means of controlling *D. antiqua* (Werling *et al*., 2006). Similarly, dressing with teflurin, while not killing *Delia* spp. larvae, also provides good control (Ellis and Scatcherd, 2007). Drenching with chlorpyrifos kills the larvae but can be phytotoxic.

3.2.2 Specialized or oligophagous feeders

For field crops the life cycles of these pests, unlike those of most generalized feeders, can be blocked by crop rotation. For orchards and plantation crops such as bananas and plantains, this strategy cannot, of course, be used. All of these pests are endopterygotes. Again, taxonomy has apparent outcomes for applied ecology.

3.2.2.1(a) COLEOPTERA; Chrysomelidae. *Diabrotica virgifera*, *D. barberi*. Corn rootworms. Consistently troublesome pests of maize in the American corn (= maize) belt, but also occurring as far north as Quebec and more recently in Eastern Europe. These insects are related to flea beetles and have some ecological similarities to them. *Diabrotica virgifera* has two sub-species, *D. v. virgifera* and *D. v. zeae* (Vidal *et al*., 2005). The former, called the 'western corn rootworm', has been moving east for several decades. Major damage is to the root system of maize, current annual losses being >US$1 billion. Adults emerge from the soil in late July and August and feed on the leaves and pollen of maize and of other plants that may be in flower. Pollen is rich in protein and consumed by many insects including bees, *Apion* weevils prior to reproductive maturation (Section **6.2.1.2(a)**), and a few butterflies and hover flies. Male and female flowers are separate in maize and the adults chew off the styles ('silks') interfering with pollination so that cobs have an incomplete set of kernels. After ~2 weeks of maturation, females disperse and lay egg batches in the soil from August until they are killed by the first frosts. In 3 months they can lay ~900 or more eggs (Chiang, 1973). Diapausing eggs have an LD_{50} (Section **10.2.3.3**) of ~1 week at −10°C and stay in the soil until the next spring, but sometimes spend two winters there. This extended diapause is more common where maize is rotated with soya beans; thus, they bridge the rotation (Gould, 1991).

Tillage methods (Section **13.2.3.5(a)**) influence beetle numbers, with no-tillage systems discouraging them. The larvae attack the small roots of maize seedlings in June, homing in on elevated CO_2 levels. Since roots supply not only nutrients but also support for the plant, attack may cause the plant to fall (lodge), become stunted and produce small cobs. Plants lodging in the wind (Gray and Tollefson, 1987) lead to various problems at harvesting. Several resistant varieties grow more roots in the face of attack. European cultivars produce the root exudate (E)-β-caryophyllene when attacked, which attracts the entomopathogenic nematode *Heterorhabditis megidis* (Rasmann *et al*., 2005), so suppressing the numbers of these beetles. They are, however, resistant to *Bacillus thuringiensis* (*Bt*) and *B. popillae* (Chiang, 1973). In the USA, *Bt* cultivars expressing a variety of protective Cry toxins (Cry3Bb1, mCry3A, eCry1Ab) have induced resistance in these beetles (Gassmann *et al*., 2009).

Growing maize continuously (monocropping) has been responsible for the increasing importance of this pest. North American cultivars do not produce (E)-β-caryophyllene, and this has probably had a contributory effect (Rasmann *et al*., 2005). A similar response has occurred with several other cereal pests (e.g. wheat midges) grown in the absence of crop rotation, although reservoir populations (Section **13.1.2.2**) are present on several weedy grasses. A return to crop rotation, often with soya beans, has provided good control of this species until recently, when a new strain of the beetle, breeding successfully on soya bean roots, evolved. Experimental work has begun using *Cuphea* cultivars (Lythraceae), which have the potential for oil production (Behle *et al*., 2008), as a suitable alternative crop. Counting adults on maize or sweep netting them on soya beans is used to predict levels of damage in the next year, but entomologists often use yellow Pherocon AM sticky traps.

3.2.2.1(b) COLEOPTERA; Curculionidae. *Exophthalmus vittatus*. Fiddler beetles. Caribbean pests of citrus roots. Some other similar short-snout weevils. These and other weevils having short rostra are often separated in the group Adelognatha (Richards and Davies, 1988). *Exophthalmus* are big weevils (~15 mm), common in Jamaica and important pests of citrus. The adults are relatively long lived. They are brightly coloured *and* polymorphic, an unusual combination. On a black background the adults have a variety of coloured vittae, or lengthwise stripes, white, yellow, orange, red or metallic blue. Similarly, the leaf beetle *Cerotoma trifurcata*, (Chrysomelidae) is yellow, tan or red with black spots. Such polymorphic but brightly coloured insects are thought to deter naïve tetrapod predators, who show *neophobia*, an avoidance of strange new objects (Brower, 1984; Mallet and Joron, 1999; Trivers, 2011; Section **10.2.3.5**), by revealing a variety of new patterns. This should be investigated for *Exophthalmus*.

Adult females are common after rains when fresh flushes of new, light green foliage appear on the trees. They each lay numerous (~2000), small eggs on these leaves which they then roll up, presumably to protect their progeny. The newly hatched (*neonate*) larvae are active, drop to the ground, burrow into the soil and attempt to locate rootlets, but predatory insects eat many of them. Since eggs are laid on terminal leaves the young larvae drop in the vicinity of the small peripheral roots upon which they feed. Due to plant sectoriality (Section **2.3.2**), fast-growing flushes are likely to correspond vertically to fast-growing, more nutritious roots. Larger larvae feed on larger roots and successful ones pupate within the soil from whence the adults emerge. The high AF suggests that the strategy of having numerous, small, searching young larvae has been selected for in preference to that of a few large ones. High fecundity is found in several other soil-dwelling pests: *Tipula paludosa*, cutworms and swift moths. But in cabbage root flies, which have rather similar larval behaviour, AF is only ~100. The aerial symptoms of attack are wilting, yellowing and subsequent death of a section of the tree, one corresponding to a moribund major root, which again is due to sectoriality. Damage may be extensive on porous soils where the young larvae are more able to locate roots, but is seldom severe on heavy clays. Fortunately, the former soils are penetrated easily by insecticides.

In Central America, *E. jekelianus* feeds on West Indian Mahogany (*Cedrela odorata*, Meliaceae). *Diaprepes abbreviatus* continues to be a major pest of citrus in Florida and the Gulf States (Lapointe *et al.*, 2006). This root-feeding weevil is spreading westwards, posing a threat to Californian citrus. In Florida, citrus sprayed monthly with a particle film ('Surround') showed enhanced growth and consequently greater resistance to this pest. Entomopathogenic nematodes have been used and would probably suppress *Exophthalmus*, as they do several diverse beetles. A similar weevil, *Pachnaeus litus*, also occurs in Florida.

Adult *Sitona* (= *Sitones*) weevils infest crop legumes in Europe and North America. They feed on the leaves characteristically excising notches in their margins, while the more numerous larvae feed on the root nodules (Jackson, 1920), a rich source of nitrogen (up to 10% dw). Heavy infestations of *S. hispidulus* on lucerne and red clover reduce nitrogen fixation and, consequently, its concentration in the leaves of these important fodder crops. *Sitona lineata* has a wide European distribution, is univoltine and may fly to overwintering quarters like *Apion* (Section **6.2.1.2**(**b**)). Exceptional females lay eggs throughout the late spring and summer and may deposit >1600 eggs on the soil. *Sitona humeralis* is found in the Mediterranean regions, while *S. discoideus* feeds similarly on lucerne root nodules in New Zealand. Some *Sitona* spp. transmit plant viruses (Fulton *et al.*, 1987). Adults are frequent hosts to the parasitic wasp *Microctonus* (Section **6.1.2.2**(**b**)). Jackson records three other braconid wasps from adult *S. lineata*: commonly *Perilitus rutilus*, and rarely *Pygostolus falcatus* and *Liophon muricatus*. The nematodes *Steinernema* and *Heterorhabditis* kill the juveniles (Jaworska and Wiech, 1988).

3.2.2.1(c) COLEOPTERA; Curculionidae. *Cosmopolites sordidus*. Banana weevils or borers. Pan-tropical pests of banana and especially plantain corms. Adults of this structurally advanced weevil, with its fine, elongated rostrum, together with their larval progeny, bore the corms of bananas and plantains, the latter being very vulnerable. Such proximity is unusual among endopterygotes, although found in some chrysomelid beetles such as *Leptinotarsa* (Section **5.2.1.2**(**c**)). Adults are all black, less robust and smaller than *Exophthalmus*. Affected plants are stunted, have a shrivelled appearance, fewer leaves than healthy ones and eventually produce only a small bunch of fruit. Large, newly infected plants (especially Gross Mishel, which may reach 8 m) are untroubled by a few borers. In general, new infestations result from planting infected suckers, the adult females having poor dispersive powers. Being flightless, they disperse at night by walking. Thus suckers should always be stripped with a machete before planting – the dark brown necrotic tunnels and the white legless larvae that make them are then easily identified and destroyed. Overall, numbers tend to be higher in the dry season. A synthetic aggregation pheromone (Cosmolure or Sordidin), often in conjunction with split pseudostem or pitfall traps, has been successful in reducing the numbers of adults (De Graaf *et al*., 2005; Duyck *et al*., 2012). They are also attracted to dead banana leaves (Braimah and Van Emden, 1999). The rustic preventative method in Jamaica is to pee around the base of the corms: hardly practical in big plantations! Another similar weevil, *Odoiporus longicollis*, mines the pseudostems of bananas in South-East Asia, reducing production and killing the suckers. Another banana pest, *Metamasius hemipterus*, is found in Central and South American.

3.2.2.1(d) COLEOPTERA; Curculionidae. *Cylas formicarius*. Sweet potato weevils. Pan-tropical and sub-tropical pests of sweet potato tubers. These small, metallic-blue weevils, often separated in the Brenthidae, lay eggs in sweet potato tubers, the stimulants for oviposition being boehmerol and boehmeryl acetate. They use the rostrum to bore in and lay eggs in the wound, behaviour often found in weevils. The boring larvae ruin tubers commercially and allow rapid spread of brown rot fungi in storage. Again, this weevil is easily dispersed with plant parts. Affected tubers are best chopped up and fed to pigs, a handy and productive receptacle for plant material contaminated by pest insects. If we contrast the commercial effect of *Cylas* and *Cosmopolites*, an important distinction emerges. While both are soil-dwelling weevils, the first attacks the marketable product, the second does not. Pests doing the former can be tolerated at much lower levels than the latter.

Two other species, *C. puncticollis* and *C. brunneus*, damage sweet potatoes in parts of East Africa, particularly in the dry season (Stathers *et al*., 2003). Farmers often leave infested roots in the field, providing a ready source of further infestation (cf. Section **5.2.1.4(a)**). This habit, which occurs in many parts of the world, occurs when people believe in luck rather than cause and effect. Nematodes such as *Steinernema* have been tried against sweet potato weevils. In the laboratory, *C. puncticollis* is susceptible to the fungi *Beauveria bassiana* and *Metarhizium anisopliae* (Ondiaka *et al*., 2008). While feeding and reproduction are suppressed, adults have an LD_{50} of 10–19 days. Infected tubers could be split and inoculated with these fungi as a control. Another weevil affecting this crop in the West Indies is *Euscepes postfasciatus*.

3.2.2.1(e) COLEOPTERA; Curculionidae. *Palaeopus costicollis*. Yam weevil. This is a flightless species with fused elytra and reduced metathoracic wings. Despite its obvious lack of mobility, it has a 1:1 sex ratio (see Hamilton, 1967), suggesting that it disperses effectively within the crop. Females lay single eggs just below the cortex of the old part of the yam used in planting out, but do not spread into the young growth that will constitute the crop, and thus cause only limited damage. But they will also breed in sweet potatoes and ginger. As in *C. formicarius*, development takes about 6 weeks.

3.2.2.1(f) LEPIDOPTERA; Gelechiidae. *Phthorimaea operculella*. Potato tuber moths. Widespread pests of potatoes, especially in warmer regions. This pest does not fit well into our ecological classification since the larvae initially mine the leaves and later bore the stems and tubers. However, since its depredations above ground cause the least damage while the tubers are the marketable product, the pest is placed here. This moth may have originated in the eastern Andes and spread with the potato, but along with another gelechiid moth, *Tuta absoluta*, it also attacks other solanaceous crops such as tomatoes (Pratissoli and Parra, 2000) and aubergines. Like wireworms, the larvae may continue to damage potato tubers in storage, leading to multiplicative effects.

Under warm conditions there can be up to 12 generations per year, but even as far north as Oregon, USA, (~45°N) there are several generations (Dogramaci *et al*., 2008). Here the moth, which has no true diapausing stage, survives the winter best as pupae, although gradual attrition occurs. These workers found experimentally that pupae deprived of their cocoons had roughly half the survival of those with them, and, unsurprisingly, those deeper in the soil lived the longest. In India, two ichneumons, *Eriborus trochanteratus* and *Agathis unicolorata,* attack this moth (Chundurwar, 1975, 1977, in Nikam and Pawar, 1993). In Brazil, inundative releases of *Trichogramma pretiosum*, which attacks the eggs, have been successful (Pratissoli and Parra, 2000). In Australia, the encyrtid wasp, *Copidosoma koehelri*, which attacks the eggs and larvae, has been released against it. The larvae also host the braconid wasps *Apanteles subandinus* and *Orgilus* *lepidus*. Females have an eversible pheromone gland at the tip of the abdomen and male numbers can be estimated using pheromone traps. Unfortunately, chemical insecticides are still often necessary to control it.

3.2.2.1(g) DIPTERA; CYCLORRHAPHA; Syrphidae. *Merodon equestris*. Onion flies. Temperate pests of onions and a few other bulbs. This is a minor but interesting pest that belongs to a most diverse and attractive family of flies in the Cyclorrhapha. It is relatively large (20 mm wingspan) and has good dispersive powers so that it presents a control problem in some ways similar to that of cutworms, although it is generally far less numerous. It is a polymorphic mimic of several bumble bee species. One or two eggs are laid on each developing bulb, which the boring larvae destroy. In south-west England and the USA it is particularly attracted to narcissus bulbs, which it also destroys. Stored onions (the marketable product) can rot completely because a few are infected by this pest: so again we see a multiplicative effect, which is typical of damaged plant products in storage. Larvae can be killed and the bulbs saved by immersing them in warm water but the temperature required, ~45°C, is critical. Species of the syrphid flies *Eumerus* and *Kumerus* attack a variety of bulbs and tubers, mainly of monocotyledons, and in parts of the tropics larvae of *Eumerus figurans* bore into ginger.

3.2.2.1(h) DIPTERA; CYCLORRHAPHA; Psilidae. *Psila rosae*, *P. nigricornis*. Carrot root or carrot rust flies. Widespread pests of carrots and other Umbelliferae, and Compositae with tap roots. These flies are small, weak fliers, with a dispersive range of <1 km. Although now found in most places where carrots are grown they are native to Europe. They attack both wild and cultivated carrots, confining their damage to the nutritious surface. *Psila nigricornis* also attacks the roots of lettuces and chrysanthemums (Compositae). In our development of carrot cultivars from their scrawny precursors, *Psila* found a dipteran paradise: its larvae consume a cornucopian food source compared to the tap roots of wild carrots (see Fig. 13.1). Even so, a large section of its population may exist in such locations, particularly as these species feed on other wild Umbelliferae such as hemlock (*Conium*) and hogweed (*Heracleum*). Hence, as with all generalized feeders, this specialized pest still has a natural reservoir of population outside of the farmer's control (Section **13.1.2.2**). Since cultivated crops have often been derived by selective breeding from wild ancestral plants living in the same area, such a situation is similarly frequent in the various pests that attack them. But because *Psila* has limited powers of flight (Jones and Jones, 1984), the problem is to an extent contained.

The females are attracted by volatile exudates from carrot foliage and lay small batches of eggs on the soil near these plants. Resistant cultivars such as Clause's Sytan Original induce little oviposition, while susceptible ones like Danvers Half Long 126 do so (Guerin and Stadler, 1984). Sytan and Regulus Imperial also have resistance to larval attack. Peak rates of egg laying occur when females are 4–9 days old. Eclosing larvae migrate through the soil and enter the cortex of the root, burrowing downwards and then upwards. They pupate a few centimetres away from the root and in temperate regions generally spend the winter in this stage, although some late larvae will continue to feed during mild winter weather. The flight periodicity may be monitored using yellow sticky traps (Hooper *et al.*, 2002). In temperate areas there are two to three generations per year, more in the Mediterranean and the tropics. In Jamaica, attacked carrots are frequently offered for sale in open markets, conveniently providing the lecturer in entomology with teaching material! Seed dressings protect against attack in early sown varieties, while in temperate regions late sowing is an alternative that reduces the depredations of this pest. Here, it is important to lift the crop in October or November and to destroy damaged roots. In horticulture, intercropping with onions deters ovipositing females.

3.2.2.1(i) DIPTERA; CYCLORRHAPHA; Muscidae; Anthomyiinae. *Delia radicum* (= *Erioischia*, = *Hylemyia brassicae*). Cabbage root flies. A Holarctic pest of brassicas. Brassicas are part of the Cruciferae; a family memorably distinguished by having flowers with petals in the form of a cross, hence their botanical name. Brassicas include swedes, cabbages, kale, cress, Brussels, sprouts, broccoli, cauliflowers, mustard and oilseed rape. Cabbage root flies are larger than *Psila* and better fliers, but as in *Psila* they maintain reservoirs of population in wild relatives of the crop plants they attack. These include wild cabbage and field cabbage, but more commonly volunteer rape at field margins (Finch and Skinner, 1975). Adults migrate when 5–6 days old, females moving as much as 3 km, but males disperse no more than ~100 m/day. In Oregon, USA, brassica fields within 400 m of existing infestations are at risk of a severe attack (Dalthorp and Dreves, 2008). But because of the greater migratory potential in *Delia* females, crops may be attacked far from pre-existing infestations, although initially at lower densities. This is expected from an insect dispersing close to the ground (Section **10.2.4.1**).

In the UK there are two annual generations. Females emerging in spring are larger (~16 mg) and more fecund (60–80 eggs) than those emerging in summer (~11 mg, 40–60 eggs). Oviposition starts when they are ~1 week old. As in other *Delia* species, *Psila*, *Diabrotica,* and many cutworms, the eggs are laid on the ground near the plants, in this case often in crevices. Heavy rain washes the eggs into the soil thus reducing predation, a good example of a physical factor influencing the action of a biotic one (Section **10.1**). The young larvae migrate through the soil and bore into the root. Predatory carabid beetles (*Bembidion* and *Trechus* spp.) often attack them heavily at this time, particularly at higher temperatures (Hughes and Mitchell, 1960) and if, due to earlier chemical spraying, the soil is depauperate in other prey (Finch, 1989). In Ontario, Canada, where there are three annual generations, larvae in the soil incur ~60–70% mortality (Mukerji, 1971). In the UK, Hughes and Mitchell's estimates are often >90%. But on penetrating the root the larvae are relatively invulnerable, maturing in 15–20 days. Under sowing with clovers increases the densities of predatory beetles, and improves soil fertility.

Aleochara bilineata and *A. bipustulata* (Staphylinidae) eat the eggs and larvae. They are extraordinary in being not only predatory as adults but also parasites of the fly's puparia when juvenile. The female beetles show a strong aggregative response, being attracted to odours from the frass of their host and also by its movement. The parasitoid larva does not prevent the host from pupating, however. It then burrows out of the pupa and feeds on it externally from within the puparium. *Aleochara* also attacks *Delia antiqua* and *D. florilega* (Section **3.2.1.2(g)**), which infest onions, and *D. floralis*, which is a pest of turnips. In the UK, *Phygadveon trichops* is another parasitoid, while *Trybliographa rapae* is a specialist cynipid that oviposits mainly in the young larvae (Jones *et al.*, 1993). Superparasitism is rare. In Ontario, Mukerji (1971) found *T. rapae* to be insignificant. Further mortality results from the death of cabbage roots, which is frequently a density-dependent result of overcrowding (Hughes and Mitchell, 1960). Poorly fed larvae form small pupae and often fail to emerge.

In the UK, final-generation pupae enter diapause from late August to October, requiring an extended period of temperatures below 5°C to complete their diapause development (Section **10.2.2.2**) and a further period above this temperature for final development (Coaker and Wright, 1963). Pupae from temperate continental regions have much greater cold hardiness than those from temperate oceanic ones (Turnock *et al.*, 1998). Thus, over 80% of Russian pupae survived at −17°C for 14 days. In Europe and Canada, there is a genetically determined polymorphism of early and late biotypes that results in an extended period during which the flies emerge (Finch and Collier, 1983), a well-researched case of risk spreading (Section **9.7**). In Canada, the details of this polymorphism also vary between the prairie states and Ontario (Andreassen *et al.*, 2010), a strategy that may have evolved to achieve a temporal refuge (Section **9.9**) in relation to the fact that *Aleochara* eats not only the fly's eggs but also parasitizes its puparia. But it makes it more difficult to devise control methods. Emerging flies may fail to reach the soil surface. Egg density in the soil tends to be higher in the first generation (Mukerji, 1971), which is similar to results from England and Holland and may relate to the differences in fecundity noted above. Using *K*-value analysis (Varley and Gradwell, 1960; see also Section **11.4.3**), Mukerji found that the loss of young larvae was the key factor and density-dependent processes operated only in the later stages of development.

Unlike the case of *Psila*, damage is not confined to the surface layers of the root, and larvae can destroy sizeable plants during their 3–4 week period of feeding, especially during drought. But apart from swedes, in most brassicas the marketable product is not attacked and hence mature plants can tolerate a moderate level of infestation. In this connection, an early sowing date improves the plant's chances of resisting attack. In the UK, oilseed rape is widely grown as a break crop between cereals. The autumn sowing of this brassica means that their roots develop and become tough during winter and so are less easily penetrated by this pest.

Compare the ecology of *Delia* spp. with that of *Psila*. In horticultural practice vulnerable seedlings should have a root dip before planting out or be planted out with a granular formulation. Recently, film-coating brassica seeds by passing them through a fine spray has been developed and requires as little as 2 g of organophosphate/ha. Such techniques protect the roots of the developing plants, while avoiding killing the beetles so important in reducing the numbers of this pest. The larvae are placed between the devil and the deep blue sea. The traditional method of putting tarred felt discs around the young plants, to prevent oviposition near them, has been re-introduced by growers of organic brassicas. Ovipositing flies can be caught and monitored in water traps, or in ones baited with mustard oil volatiles.

3.2.2.1(j) DIPTERA; CYCLORRHAPHA; Muscidae; Anthomyiinae. *Delia* (= *Leptohylemyia*, = *Hylemyia*) *coarctata*. Wheat bulb flies. European pests of underground cereal stems. This is another grey and bristly fly found mainly in Central and Northern Europe where it can be a significant pest of wheat and barley. There are oddities of the life cycle, as follows. Adults fly in June and July and lay about 50 eggs on bare soil. Oddly, these eggs diapause until mid-winter, suggesting that they have an ability to resist both desiccation and cold and require both summer and winter diapause (see Hinton, 1969). They hatch in January and February, but need a temperature a little above freezing for eclosion. This may be delayed by severe weather. Young larvae wander through the soil and enter underground stems of late sown winter wheat or early sown spring wheat, attracted by root exudates. Successful larvae feed in the base of the shoot causing it to swell and turn the tiller yellow. They feed actively, each one damaging several plants. Mature larvae pupate in late spring and emerge ~6 weeks later. There is only a single annual generation and so the potential for increase is less than in *Delia radicum* or *D. platura*.

The timing of oviposition and its location in bare soil is a weak link that can be used to manage this pest. If it is known to be a threat, either by experience, by watching oviposition or by sampling the eggs, there is time in autumn to switch to a non-susceptible crop such as oats, oilseed rape or potatoes. All the young larvae then die. Alternatively, more sophisticated sampling of egg densities by an advisory service can establish thresholds for spraying in springtime. If winter wheat is sown early in October, the plants will be normally sufficiently established, with two to four tillers in February, to resist attack. If it has to be sown late then one should use dressed seed if there is an expectation of attack. Spring wheat is unaffected as long as it is planted a few weeks after eclosion. The pest, therefore, does not pose insuperable problems even when cereals follow cereals. Also, Bardner *et al.* (1973) in a 9-year study at Rothamsted, UK, found that only ~1% of shoots were initially affected although, as we noted, older larvae may attack additional ones. *Tetanops myopaeformis* (Diptera, Ulidiidae) infests roots of sugar beet in mid-western North America. It attacks only *Beta* and *Atriplex* (Chenopodiaceae), but it may multiply slowly in low-temperature storage (Yocum *et al.*, 2012).

3.3 Sucking Pests

3.3.1 General introduction

This section contains only a few homopteroids, a group showing a gradual evolution of closer association with the plants they attack. Sucking insects may inject substances into the plant to modify its physiology, an extreme example being gall formation by various aphids. Alternatively, the plant may respond by localized necrosis or other defences (Section **2.4.2**). While feeding by sucking probably originated with the extinct Palaeodictyoptera in the late Carboniferous, it became more developed with the Hemiptera in the Jurassic (Scott *et al.*, 1992) or earlier. The Auchenorrhyncha probably date from the Upper Permian (Moran, 2007). Several homopteroids come from Jurassic deposits at Karatau, Kazakhstan, dated at 152–157 million years ago (Labandeira, 1997). A graded series exists in the Auchenorrhyncha from the structurally less modified Triassic groups (cicadas, cercopid, membracid, cicadellid and fulgorid bugs), through to the Sternorrhyncha (Psylloidea, Aleyrodoidea, and aphids, adelgids and various scale insects). In the last three groups peculiarities of the life cycle develop, particularly an alternation of sexual and asexual generations, alternation of food plants, parthenogenesis, and even hermaphroditism, which we will examine shortly. All homopteroids are closely adapted to the low nutritive value of their food, phloem sap has <0.5% nitrogen (dw) and xylem sap even less (Mattson, 1980b), and probably all of them employ endosymbiotic micro-organisms.

3.3.2 AUCHENORRHYNCHA; Cercopidae, Cicadidae

3.3.2.1(a) AUCHORRHYNCHA; Cicadidae. Cicadas. Large, noisy bugs, Mediterranean and tropical pests of tree roots. Like some cercopids, cicadas have adults that live above ground and soil-dwelling nymphs. But cicada nymphs usually live there for several years, sucking the dilute fluid from the root xylem. In North America, some cicadas have 13-year and others 17-year life cycles (*Magicicada tredecim* and *M. septendecim*). The 'dog-day cicadas' that become adult under hot, humid conditions in summer, have a cycle of only 2–5 years. The population density of *Magicicada* nymphs in *Ulmus*/*Celtis* forest in eastern North America has been estimated at >600,000/ha (Dybas and Davis, 1962). Large nymphs construct earthen cells. Such high, periodic densities retard tree growth and leave traces of their attack in the rings. This bug is host to the pathogenic fungus *Massospora cicadina*, while *M. levispora* infests the cicada *Okanagana rimosa* in Ontario (Soper *et al*., 1976).

One of several joyful features of travelling through the country roads of France towards the Mediterranean coast is the sound of cicadas (*Cicada orni*, *Tibicen haematodes*) as one nears the destination. The result of their stridulation is not always so joyful, however, for in North America calling by male *O. rimosa* attracts not only mates but also the sarcophagid parasitoid *Calcondamyia auditrix* (Soper *et al*., 1976). As in most *Tipula* spp., cicadas often emerge *en masse*, which could result in predators being satiated and hence a reduced risk to individual bugs (Corbet, 1964; Lloyd, 1984; Cooley *et al*., 2001; Section **9.9**). Although nymphs do the most damage, females feeding and ovipositing on the twigs of trees and shrubs also contribute. In southeast China the large and abundant *Cryptotympana* damages camphor, tung and a few other trees (Hill, 1997). Cicadas are often pests of top fruits, such as apples and plums, but also of decorative horticulture.

3.3.2.1(b) AUCHENORRHYNCHA; Cercopidae. *Aeneolamia* spp. Sugar cane froghoppers. Neotropical pests of sugar cane. Adult cercopid bugs are masters of immediate escape, having milligram for milligram, the most powerful jump among the insects. They have a locking mechanism for the hind legs under the thorax, which is released only when sufficient muscular tension is built up, exerting a force more than 100 times their body mass. The reason for this remarkable ability is a mystery as several species are warningly coloured black and red! But it may be a fail-safe mechanism in which, if the first line of defence fails, the second is brought into operation. Several other such systems are known, for example the presence of sinister images on cryptically patterned moths (Trivers, 1985; see also Section **5.2.1.3(b)**). All cercopid nymphs live in the soil (Strong *et al*., 1984).

Females lay most of their eggs in the soil although, oddly, a few may be deposited on aerial parts of the plant. There are generally only four overlapping generations annually, but in the south of their distribution in Argentina and Chile there may be only two, the eggs diapausing for several months. Most nymphs feed on the roots, out of sight and mind. Adults may be as much as 8 mm long and their feeding on the leaves causes necrotic spots, yellowing and stunting of the plant. Cane is very resistant to insect attack when well irrigated, however. While these bugs may be found commonly on this crop, they generally do little damage as a whole because other plants fill in any gaps. In the past, cane fields have been dusted from the air with DDT, γ-BHC or carbaryl. But unnecessary spraying may upset the normal balance between a potentially serious pest of cane, the lepidopteran borer *Diatraea* (Section **4.4.3(a)**), and its effective braconid parasitoid *Apanteles flavipes*.

Other Neotropical genera include *Tomaspis*, *Delassor* and *Marhanava*. Formulations of the fungus *Metarhizium anisopliae* (Section **13.2.4.5**) have been used against the last-named bugs in Brazil. The genus *Locris* is found in Africa, and *L. rubens* may be a pest of sorghum in west and central regions. In *Philaenus spumarius*, the spittle bug, the nymphs feed above ground and cover themselves with a frothy coat secreted from the anus. In eastern North America they can cause damage in clover fields (Section **12.3.4.3**).

3.3.3 STERNORRHYNCHA; Aphidoidea; Aphididae

The Aphididae are a particularly important family of plant pests. The Eriosominae spend much of their life cycle attacking plant roots, while the larger group, the Aphidinae have only a few genera that do so. Although aphids are more significant in temperate environments than in tropical ones, several notorious species are found worldwide.

In addition, there are some damaging tropical genera like *Toxoptera*, the citrus aphids. Not only do they attack a wide variety of crop plants directly, often killing terminal foliage and hence destroying apical dominance, but they are the most important insect vectors of plant viruses, known to transmit >275 viral species in 19 genera (Nault, 1997). Hence, we will deal with them in some detail.

3.3.3.1(a) STERNORRHYNCHA; Aphididae, Eriosominae (= Pemphiginae). *Pemphigus bursarius*, *P. betae*. Temperate pests of lettuce and sugar beet, respectively. Some aphidiine root aphids. While the majority of aphids are considered in Section **5.3.1.2(g)**, we note a few generalities here in *Pemphigus*. These intriguing insects have the fully developed, complex (*holocyclic*) life cycle typical of several aphids in temperate environments, in which two dissimilar plant species, or groups of species, are utilized: a woody winter plant and a herbaceous summer one. While there are differences in detail from the cycle in aphidiine aphids, all parthenogenetic aphids are viviparous (Blackman and Eastop, 2000), so the cycle here serves as a general introduction. In autumn, sexual reproduction occurs, the *oviparae* laying single eggs on the woody food plant. These hatch at bud burst in spring to give one or more generations. Alate morphs then migrate to the summer plant where several more generations occur until the sexual forms appear again in autumn. Sexual reproduction occurs just prior to the onset of harsh weather, as is common where alternation of these two reproductive modes occurs. It also allows accruing deleterious mutations to be eliminated (Charlesworth *et al*., 1993). This pattern, called *cyclic parthenogenesis*, involves two migratory phases (Moran, 1992b). In other aphids, especially tropical ones, the complexity of the cycle is reduced (*anholocyclic*), normally by the suppression of the sexual stages, and in a few pest and non-pest aphids there is only a single food plant.

The Eriosominae, which also includes the woolly aphid *Eriosoma* that cankers apple trees (Section **4.3.2**), are characterized by the fact that the sexual females each produce only one large egg. It is a small sub-family containing ~300 world species of which ~70 are in *Pemphigus*. All these species overwinter on poplar (Blackman and Eastop, 2000). *Pemphigus bursarius* and *P. betae* remain there as eggs on the trunks, particularly those trees, like the Lombardy and black poplars, which have deeply fissured bark. This location places them out of the reach of most small, avian predators, particularly the Paridae or titmice, although the coal tit, *Parus ater,* sometimes feeds in such locations. Tree creepers (Certhiidae), however, which search trunks for insect food during the winter, probably eat them. Along the Canadian/USA border *P. betae* is associated with the distribution of *Populus angustifolia* (Harper, 1963). Being tall and quick to grow poplars are often planted as windbreaks (see **Fig. 13.15**). In France, they provide shade along many major roads and are grown in damp situations for timber, so increasing the *carrying capacity of the landscape* (Section **12.3.4.4**) for this aphid.

At bud burst, the eggs, after a period of diapause development at low temperature, hatch to produce nymphal *fundatrices* that disperse to the twigs. In *P. betae* these morphs frequently contest possession of the base of potentially large leaves, with bigger nymphs being more successful (Whitham, 1980) and probably explaining the peculiar occurrence of a single large egg per mother. In the UK, bud burst is in mid-April, in Alberta, Canada, ~2 weeks later (Harper, 1963). Preferred leaves have low levels of phenolic glycosides (Section **2.4.2**). Sucking the young leaf causes it to swell into a gall enclosing the young *fundatrix*. She becomes large, globular and, continuing feeding, gives birth to clones of 100–250 genetically identical daughters or *fundatrigeniae*. Reproduction is similar in *P. betae* (Harper, 1963). Their production is under genetic control and their numbers determined largely by leaf quality. The trees, however, may reduce their load of aphids by excising affected leaves. Where there are several galls per leaf, numbers per gall are reduced, a very clear case of resource competition (Sections **9.8** and **10.1**). Some syrphine larvae, anthocorid bugs and in Canada small coccinellid *Scymnus* beetles eat them. In June, they fly off into the wide blue yonder, but the ones emerging earlier are larger and potentially more fecund than those emerging later. Like many aphids they are attracted by white and short-wave light emanating from the base of cumulus clouds. After spiralling upwards and being displaced on the wind their response to light changes, longer wavelengths being selected, and they settle. Iterative searching for the food plant then usually occurs, but the whole process doubtlessly leads to great attrition (Taylor, 1977; Ward *et al*., 1998).

In *P. bursarius*, successful migrants, a minute fraction of the total, begin to feed on lettuce roots or on those of a few related and widely distributed plants like *Sonchus asper* and *Taraxacum officinale* (Compositae). So these weeds house natural reservoirs of the pest (Section **13.1.2.2**), although the individuals are smaller than those on lettuce. Nymphs are produced mainly on the aerial part of the plant but quickly seek the roots. Two to four generations of these *alienicolae* pass in the production of clones by successful females. Densities >60,000/m^2 can occur and roots acquire a waxy, mealy coat. In *P. betae* in Canada, *Scymnus* spp. feed in these aphids in the soil and so do larvae of syrphine flies such as *Metasyrphus* and *Scaeva*. But their effectiveness as predators is reduced by parasitism from *Diplazon* and *Syrphoctonus* spp. (Ichneumonidae) and the pteromalid wasp *Pachyneuron syrphi* (Harper, 1963).

In August and September, a final generation of alienicolae produces winged daughters, the *sexuparae*. Here, a change to the alate form is environmentally controlled in response to crowding or to diminishing food quality. Rainy weather at this time, however, causes the soil particles to swell, imprisoning many alates, a physical factor having sequential mechanical effects (Section **10.1**). Free sexuparae fly to the poplars in September and October, where each produces 2–5 males and oviparae. Again, very few of these migrants will locate poplars, but as we saw, their chances are increased by our various uses of these trees. Since the sexual forms may be the progeny of different mothers, genetic mixing occurs. They are strongly thigmotactic, penetrating deeply into the fissured bark. After mating, females lay a single egg, an odd case in which sexual reproduction leads to a decrease in population size. Sometimes specialized overwintering morphs, which develop in response to low temperature, stay behind on the roots of the summer food plants, a further instance of risk spreading (Section **9.7**).

Some points in the *Pemphigus*' life cycle are of general interest for aphid ecology. First, the winter is spent on a woody, *permanent*, food plant. Laying eggs on plants that would decay or be killed by frost would lead to great attrition. Eggs of several aphids including *Aphis fabae*, *Myzus persicae*, most fruit tree aphids (Section **5.3.1.2(h)**) and those of many moths, overwinter on bark, branches or twigs. While the physical environment is harsh, the levels of predation are likely to be low, although as we noted a few insectivorous, resident birds eat some of them. Second, a clone on both food plants exploits fast growth. Finally, sexual reproduction occurs before winter, the period of adversity, and is an example of the key distinction between asexual and sexual reproduction: the former is for increase, the latter for the genesis of variability. Erasmus Darwin (1800) wrote: 'From the sexual … generation of plants new varieties … are frequently obtained; as many of the young plants from seeds are dissimilar to the parent ... sexual reproduction is the … masterpiece of nature'.

If *Pemphigus* is a continuing problem, insecticides such as diazinon can be rotovated into the soil prior to planting out. In the UK, late spring-sown plants are vulnerable. As in cabbage root flies, pest attack is most serious on young plants during drought. Copious irrigation reduces successful attack and alleviates the symptoms. Some lettuce cultivars such as Avoncrisp show considerable resistance to attack. This is often associated with high levels of isochlorogenic acid and the enzyme phenyl alanine-ammonia lyase in the roots. *Pemphigus betae* feed on the secondary roots of beet and may reduce sugar production by 40%. It also transmits the viral diseases Curly Top and Virus Yellows. Other similar species in North America are *P. populi-transversus* and *P. nortoni*, while in Eastern Europe and the USA, *P. fuscicornis* is found on sugar beet. *Trama troglodytes* feeds on lettuce roots but is larger and does not secrete wax.

Several aphids are found on fodder grass and cereal roots, but have been little studied (Eastop, personal communication). *Aploneura lentisci* attacks such plants but overwinters on pistachio nut trees in Mediterranean regions, while another cereal root aphid, *Anuraphis maidiradicis* attacks maize and is spread by *Lasius* ants. Indeed, most species of root-feeding aphids have a symbiotic association with ants. *Rhopalosiphum rufiabdominalis* infests rice roots, *Aphis forbesi* strawberry roots and *Dysaphis tulipae* tulip bulbs. *Prociphilus piniradicivorus* sucks the roots of *Pinus* spp. but its economic impact is difficult to assess.

3.3.3.1(b) STERNORRHYNCHA; Coccoidea, Stictococcidae. *Stictococcus vayssierei*. Cassava root mealy bug. A new West African pest. Cassava provides staple food for more than 300 million people worldwide. This bug appeared in Cameroon and the Central African Republic in 1979 and later in Congo, Gabon and Equatorial Guinea. Its origin is unknown (Ngeve, 2003). During this spread it became more numerous and was found on the roots of a variety of crops including bananas, maize and groundnuts. Nymphs and adults attack the young roots of cuttings causing leaf fall and frequent death, often killing entire plantings. While a few cultivars show some resistance, even in the best the majority of plants die. If they survive, later on the root crop becomes smothered with these bugs, rendering them unsaleable. Attack is particularly severe during the dry season and in mixed cropping. At present, affordable methods of disinfesting the cassava stakes prior to planting out need to be developed.

4 The Pests of Plant Stems

4.1 General Introduction

Stems are the basic, axial component of plant architecture (Section **2.3.2.2**), providing support for the aerial structures. They contain the plant's transport or *vascular system*, piping water and nutrients from the soil in tracheids and xylem vessels, and sap in phloem vessels. Occasionally lateral adventitious stems, like runners in strawberries and mint, effect asexual reproduction. In perennial trees and shrubs, the stem becomes woody by *secondary thickening*, essentially proliferation of the xylem. Two concentric cylinders of actively dividing tissue are involved, an internal *vascular cambium* forming xylem on the inside and phloem on the outside, and an external *cork cambium* forming the bark (Fig. 4.1). The xylem becomes a heavily lignified structural support and the protective bark becomes impregnated with a waterproof called *suberin*. In all there is dead, protective bark, living *bast*, sapwood and dead heartwood. Only the bast is at all nutritious. Non-woody stems are naturally simpler in structure and found in annual and biennial plants.

Stem systems are variously affected by pest insects. The great majority are biting, internal pests, gaining protection as well as nutrition from the plant they attack. They are best sub-divided as pests of *woody* or of *non-woody* stems. Woody stems comprise the trunks and branches of forest or orchard trees, while non-woody stems are mainly those of cereal crops and grasses, less frequently those of other crop plants such as legumes. Like root systems, stems (particularly woody stems) often provide long-lasting resources. Thus several insects attacking the latter have long life cycles. Also, damage to all organ systems above ground may be affected by cryptic insect and nematode damage below it (Brown and Gange, 1990).

The ecologies of internally feeding pests in woody and non-woody stems are naturally quite different, not only because the former are often massive, complex and relatively permanent, while the latter are not, but also because of the presence or absence of lignification itself. Lignified tissue is dead, providing poor quality food (nitrogen <0.2% dw) and insects attacking it probably all carry symbiotic fungi or other organisms as a means of breaking it down (Martin, 1991). On a gross scale, woody stems occur largely in forests and orchards, whereas soft stems are in fields. Unsurprisingly, the taxonomic groups and sizes of insects involved are different. The former comprises termites, boring caterpillars and a variety of larval and adult beetles, some of which are very large. Indeed, the most primitive beetles may have been wood borers (Crowson, 1975, in Scott *et al*., 1992). In soft stems mainly small larval Diptera, especially Cecidomyiidae and Cyclorrhapha, dominate. Even so, the weakest link in their life cycles, when they are most vulnerable to our control, is at their point of entry to the plant. Externally feeding pests are relatively few, comprising some sucking feeders such as aphids and scale insects on both woody and soft stems. While biting pests of stems are generally concealed, all the sucking pests are primarily external, although they are sometimes partly enclosed in a gall. We will consider, as usual, the biting pests first. We use a taxonomic classification within each sub-section, a scheme revealing further generalities.

4.2 Biting Pests of Woody Stems

Woody stems then, comprise two distinct microenvironments: (i) the nutrient-rich living complex of phloem and cambium; and (ii) the nutrient-poor, lignified and largely dead, heartwood. In a tree it is this mass of dead heartwood that provides its structural support both in compression and in resisting the lateral forces that strong winds impose. For example, in yew trees, the woody tissues (tracheids) have spiral thickenings that allow both the trunk and branches to support a heavy mass of leaves during strong winter winds. This makes the

Fig. 4.1. Transverse section through a tree trunk showing the various concentric areas. Two generative layers exist: one forming the wood, centrally, and another generating the bark. The width of the rings in the wood indicates conditions for growth in a particular year and so are a temporal trace record. Source: Wikimedia Commons, author Biswarup Ganguly.

wood particularly tough and springy and it was used to construct English long bows. Pests attacking the heartwood, unless they can gain direct access through a wound, must pass through the bark and the living tissue on their way in, and survivors often pupate just under the bark on their way out. Hence, they damage both microenvironments that the tree comprises and facilitate access by microbes and fungi. We will deal with all biting pests of woody stems as a unit, while remembering that two distinct regions exist. But insects that bore living tissue around trunks and branches, thus girdling them, cause greater damage than those that do not have this behaviour. Whether trees are solitary, marginal or embedded in forest also affects the microenvironment within them. Naturally, exposed trees experience greater physical variation (Section **12.2.4.3**).

Insects derived from this second group of pests in standing trees may infest furniture and structural timber in domestic situations and stores. They tend to be less specific than those attacking living trees (Nair, 2007). When we consider pests of stored grain and other plant products (Section **6.3.1.2**), we will find that there is a similar relationship to this with the insects attacking them in the field and in stores. When we bring products such as wood and grain into closer association with us, many of the pests from the wild have adapted to the new surroundings in houses, stores and silos. As we achieve a more developed domestic behaviour these insects evolve in parallel, reminding us again (Section **2.1**) that for insect populations there is no *status quo:* they are generally capable of rapid evolutionary responses to changing conditions (Denison *et al.*, 2003).

Some pests here, such as most termites, attack dead wood, although other termites affect living wood or forage for plant litter. Some insects, like many bark beetles, specialize in weakened trees or dying tissue in recently felled timber. Finally, there is a group that characteristically infests healthy trees, and these must breach the plant's natural ramparts. Generally, the mouthparts, either biting or sucking, are used to do this, although a few species employ specialized ovipositors. While plants do not have advanced immune systems like those in higher animals, trees in particular have well-developed defence systems (Section **2.4**). If they did not, they could not survive to the age that many of them do.

4.2.1.1 Exopterygota

4.2.1.1(a) BLATTODEA; Termitoidea. Termites. Tropical and sub-tropical pests of structural timber and occasionally of trees (~3000 spp.). Termites are mainly tropical, although a few species penetrate Mediterranean regions, and in the USA even further north. Their name derives from the Latin *termes*, which was applied to all wood-destroying insects. Apart from their status as pests, they are important as soil formers (Section **8.2.4**), attacking dead limbs and branches in natural forests. It is a meaningful shorthand to regard them as social cockroaches (Grimaldi and Engel, 2005; Nalepa, 2015). Indeed the North American cockroach, *Cryptocercus punctulatus*, feeds on dead wood under bark. It is sub-social and has symbiotic flagellates in its gut similar to those found in primitive termites. Some cockroaches and termites also contain the endosymbiotic bacterium *Blattabacterium*. In one primitive termite, the north Australian *Mastotermes darwiniensis*, the eggs are laid in a cockroach-like ootheca.

Beginning students must remember that termites are unrelated to ants. They are exopterygotes and ants are endopterygotes. Their development and social structure are entirely different. Unlike ant nests, termite nests are founded by a queen and a king, usually during the rainy season. It is probable that most of these early nests fail, as they are thought to in social bees and wasps. The few that do succeed produce large numbers of nymphs of both sexes, most of which develop into workers. In the social Hymenoptera, workers are always female. In primitive termites, colony size may be <1000 workers, but in advanced ones >1 million. Workers often live 2–3 years while the royal couple may survive for 15 years, so that for insects they have very long lives. In some species there are supplementary reproductives. The eusociality of termites is largely unrelated to their genetics (Thorne, 1997), but in the social Hymenoptera it is the driving force. Termite sociality evolved from ecological and life-history imperatives: their confined environment with ever-present food, nitrogen shortage (White, 1993) and their slow rate of development resulting in generational overlap, their iteroparity and high-risk during dispersal. Sharing endosymbionts for cellulose digestion is another major factor of the social life of the colony (Nalepa, 2015; Section **10.2.2.6**).

Termites are saproxylic (Abe and Bignell, 2000; Grove, 2002), digesting the cellulose in dead wood and other plant products via the indirect route of myriad flagellate protists (*Trichonympha*, absent in the higher Termitidae) and other microbes, especially bacteria, symbiotic in their guts. The protists engulf wooden particles, fermenting the cellulose to acetic acid, which is absorbed in the hindgut and oxidized to release energy. Such digestion is almost 100% efficient. Some Rhinotermitidae even have nitrogen-fixing bacteria too. The evidence for cellulose digestion independent of symbionts is fragile (Martin, 1991). Cannibalism is frequent (Wilson, 1971). All instars of soil termites desiccate rapidly in dry air. Associated with this, the workers build raised tunnels from faecal material and/or soil cemented together by the secretion of a special cephalic gland. Naturally, the tunnels reveal the foraging routes, allowing rapid identification of the pest. In Australia, the activity of subterranean termites has been studied using sensitive geophones (Mankin and Benshemesh, 2006).

4.2.1.1(b) ISOPTERA; Kalotermitidae. Dry wood termites. Termites that nest in dead trees or in wooden structures above the ground are 'dry wood termites'. Infestation often follows from a royal couple flying into a building and finding unprotected material. The colony size is <3000 individuals. In the Mediterranean, *Kalotermes flavicollis* attacks old trees and grapevines. In the Gulf States of the USA, *Cryptotermes domesticus* infests structural timber and furniture, while *Incistitermes minor* is the western dry wood termite. *Neotermes tectonae* is a pest of teak (*Tectona grandis*) in Java, living within the trunk and branches. It bores growing stems and causes swellings, and of course considerable economic loss.

4.2.1.1(c) ISOPTERA; Mastotermitidae, Rhinotermitidae, Termitidae. *Amitermes, Coptotermes, Macrotermes, Nasutitermes, Reticulitermes, Rhinotermes*. Mainly soil-nesting termites. Paradoxically, it is largely from the soil that the major damage (>90%) to structural timber of buildings originates. Those species such as *Mastotermes bellicosus* and *M. natalensis*, which build conspicuous mounds, are easily destroyed (Gray, 1972). But many of the other genera, while foraging above ground, construct diffuse subterranean nests and so are less easy to combat. Some *Nasutitermes* spp., such as *N. nigriceps*, make carton nests around branches, although the royal couple is confined to the woody part of the nest (Clarke and Garraway, 1994). But the infestation of buildings from soil-dwelling termites is due mainly to inappropriate design. While the first rule of architecture is that the building should suit the site, the second rule in areas where termites abound is that building construction must take their potentially destructive presence into account. In particular, *no wooden structure should be in contact with the ground*, thus forming a termite highway to the roof. Door jams should finish above tiled floors, not go through them. Indeed, it is preferable to have a 5 cm layer of concrete as the base (not the foundation) of a house, even under tiles. It is a small one-payment insurance. No wooden structures in lower stories should be in contact with the structural timber in a roof. While treated timber is ~10% more expensive than untreated timber, home buyers would do well to insist and check that it is used. If these precautions are carried out it only remains for a continuing watch to be kept for termite galleries snaking their way from the ground. There should be no route by which these tunnels could ascend unseen and it is well to remember that uninhabited buildings are the most vulnerable to this kind of attack. If precautions are not taken, attacks on timber-framed buildings can be devastating. Roonwal (1958) in Gray (1972) records that the Indian town of Shri Hargobindpur had to be abandoned when 400 of 1900 houses collapsed after *Heterotermes indicola* (Rhinotermitidae) moved in.

Timber varies in its susceptibility to termites, with teak and ironwood (*Eusideroxylon zwageri*) being resistant. Infected buildings must have the soil beneath them fumigated and defective timber replaced. We need to conserve forests and much is to be said for replacing traditionally wooden building materials (although these are a carbon sink) with others such as steel, aluminium, concrete and *durable* plastic, in areas where termites abound, a substitution also reducing fire risk.

Reticulitermes lives in the North Temperate Zone, with *R. chinensis* in eastern Asia and *R. flavipes* in the USA. The European *R. lucifugus* is circum-Mediterranean, but only occasionally invades buildings. *Coptotermes* is pan-tropical, with *C. intermedius* and *C. amanii* common in Africa and *C. gestroi* and *C. havilandi* found in the Indo-Malaysian region. *Coptotermes formosanus*, which was originally east Asian, is now widespread and occurs in Africa, Australia and the USA. In Malaysia, *C. curvignathous* attacks sapling *Acacia* trees after planting out and several termite species, including *C. frenchi* and *C. acinaciformis*, similarly attack *Eucalyptus* in Australia. In the latter species a colony formed in one tree may infest others within a 40 m radius. In India and Brazil, *C. heimi* and *C. testaceus*, respectively, are reported from *Eucalyptus* (Nair, 2007). *Mastotermes darwiniensis* and *Porotermes adamsoni* also kill Eucalyptus in Australia, the latter in the Great Dividing Range, while the former also destroys a high percentage of exotic *Pinus* in the Northern Territory (Gray, 1972). *Rhinotermes* spp. are found mainly in South America. Members of higher termite groups, such as the Macrotermitinae and the Nasutitermitinae, may also attack timber.

4.2.1.2 Endopterygota

These pests occur in the Coleoptera Polyphaga, the Hymenoptera Symphyta and the Lepidoptera. The presence or absence of biting mouthparts in the adults of these groups (Section **1.3.1**) affects their life history in woody tissue. In the last two groups, boring is confined to the larvae. But in adult Coleoptera, all of which have biting mouthparts, oviposition often follows boring by the adults. Jawless adult moths deposit eggs on the surface of the tree and rely on their larvae to bore in. Siricid wood wasps have ovipositors capable of piercing bark (Spradbery, 1977), but such organs are absent in the Lepidoptera. Endopterygote larvae, after chewing though the plant's tissue, often pupate within the protective casing of its stem, but Lepidoptera pupate, allowing adults, which have no biting mouthparts, to escape easily, although the pupae normally possess cutting apical spines. Adult Hymenoptera and Coleoptera, with their effective biting mouthparts, face no such difficulty.

4.2.1.2(a) COLEOPTERA; Polyphaga. The beetle species of this group that bore the wood of living trees are so numerous that it is possible to consider only a few of them. It has been estimated for a German forest that >50% of the beetles are involved in the degradation of dead woody tissue (saproxylic). These beetles often use enzymes sequestered from fungi and/or produced by bacteria in the hindgut to digest cellulose in the wood they bore (Martin, 1991). Many such beetles are spread by international trade in timber and special techniques, both pre- and post-importation, must be further developed to reduce this (Skarpaas and Økland, 2009). We will deal with representative species from the Buprestidae, Bostrychidae, Anobiidae and Curculionidae, but treat the Cerambycidae and Scolytidae more extensively. See Richards and Davies (1988) and Borror *et al.* (1989) for minor groups of saproxylic Polyphaga, and Solomon (1995) for a guide to North American borers.

4.2.1.2(b) COLEOPTERA; Buprestidae, Bostrychidae. Jewel or metallic wood-boring beetles. A variety of pests of forests and orchards. Eggs are laid in chinks in the bark and the young larvae bore into the bast. The beetles are attracted to their favoured trees by a variety of stimuli, including the reflectance of the bark (Campbell and Borden, 2005), by volatile compounds specific to the tree and to conspecific aggregation pheromones. The thorax of buprestid larvae is characteristically expanded and flattened, a simple feature distinguishing them from those of the Cerambycidae. Several species cause damage in the USA, including the widespread *Chrysobothris femorata*, an annual species that affects a variety of trees but especially top fruits. Its eggs are laid under flakes of bark. Young larvae bore the sapwood, larger ones tunnel in the heartwood. This species often damages silver maple, *Acer saccharinum*, in agro-forestry plantations in central north USA (Coyle *et al.*, 2005). *Chrysobothris mali* is the equivalent Pacific Coast species. *Melanophila fulvoguttata* attacks hemlock trees (*Tsuga*). Some *Agrilus* spp. bore blackberry and raspberry canes causing ‘gouty-gall’ and others make galls within wood. *Agrilus anxius*, the bronze birch borer, affects marginal stands of white and paper birch. Attack often starts at the tree’s apex and if not checked by cutting off the infected part, moves down. In North America, the invasive *A. planipennis* bores ash trees. In parts of the Alps, *Phaenops cyanea* attacks weakened pine trees (Wermelinger *et al*., 2008). In the tropics, *Chrysobothris* spp. are widely distributed. *Buprestia geometrica* bores deeply into tropical pines. *Belionota prasina* is distributed in Africa and the Orient, attacking a variety of commercially important timber trees (Nair, 2007). Woodpeckers eat superficial boring beetles, so that forest practice should ensure them nesting sites. In North America, woodpeckers of the genera *Dendrocopus* (commonly) and *Melanerpes* (occasionally) feed on a variety of such beetles. In California, woodpeckers reduced populations of *Dendroctonus* directly by ~32% (Otvos, 1965), while their activities, unexpectedly, increased the effectiveness of parasitoids (*Roptrocerus* and *Cecidostiba*) by a factor of about four.

The wood-boring larvae in the Bostrychidae resemble those in the Anobiidae (Section **4.2.1.2(c)**) and do similar damage. In India, the genera *Sinoxylon* and *Dinoderus* are destructive of felled timber (Richards and Davies, 1988). In some species the males show polymorphic variation in their elytral spines, a polymorphism that is probably associated with behavioural differences (Hamilton, 1996).

4.2.1.2(c) COLEOPTERA; Anobiidae. *Xestobium, Ernobius*, *Anobium*. Death-watch and furniture beetles. Cosmopolitan pests of structural timber and furniture. These beetles bore into various wooden structures wherein they breed. The larvae have greatly expanded thoracic segments. Some hardwoods (teak, mahogany, greenhart), however, are naturally resistant. Keeping furniture polished externally, and regularly treating unpolished inner surfaces with preservative, although rarely done, is a complete deterrent. These beetles have caused immeasurable damage to the timbers of historical buildings and to high-quality period furniture. *Nacerdes melanura* (Oedemeridae), the wharf borer, is an odd, cosmopolitan beetle that infests wooden structures in contact with sea water.

4.2.1.2(d) OTHER WOOD-BORING BEETLES: The Big Picture. In the higher echelons of the beetles there are two huge families that attack standing trees, the large (generally 10–50 mm), elongate longicorn beetles (Cerambycidae), and the small (generally <5 mm), compact bark beetles (Scolytidae). Adult longicorns are parallel-sided, have long antennae and do not bore. Adult bark beetles are cylindrical, effective borers, being responsible for >50% of all natural deaths of conifers in North America (Raffa and Berryman, 1987). They have been researched extensively (Rudinsky, 1962). The juveniles of both families tend to be more common in bast, although exceptions exist. Ambrosia beetles (Platypodidae) are small, elongate and related to bark beetles, but they tunnel into the heartwood where they propagate and feed on symbiotic fungi. All of these insects attack cut and felled timber accelerating its degradation, just as *Sirex* larvae may do (Section **4.2.1.2(j)**). In general, low-density timbers are more susceptible than high density ones.

4.2.1.2(e) COLEOPTERA; Cerambycidae. *Batocera*, *Desmocerus, Dirphya, Hoplocerambyx*, *Monochamus*, *Oberea*, *Saperda*, *Xylotrechus*. Longicorn beetles. Forest and orchard pests (>20,000 spp.). Cerambycid beetles are often specific to one or a few related tree species, although *Stomatium barbatum* and *Xylotrechus smei* attack many. Bark itself is remarkably diverse, protecting the tree against fire and excessive insolation as well as the incursions of diverse animals. Unsurprisingly, there are numerous cerambycid species in the tropics, many of which are unnamed or known poorly. Four large sub-families, Prioninae, Lamiinae, Lepturinae and Cerambycinae, exist. Females use their sharp mandibles to chew pits in the bark, wherein they lay eggs. Larvae are of two types, those that are flattened and bore superficially in the bast and those that are cylindrical and attack the heartwood. The former often girdles the tree while the latter weakens its structure. Species that tunnel into the tap root of seedling trees, like the polyphagous *Celosterna scabrator* in India (Gray, 1972), are also known. Some, including the maple borer, *X. aceris*, make galls, while in the Indian region *Dihammus cervinus* causes canker of young teak. Many of them, however, are important in the formation of forest soils. Several, having brightly coloured adults, are diurnally active and often found feeding on pollen. Linsley (1959) reviewed their general ecology and Allison *et al.* (2004) their chemical ecology. Some such as *Monochamus* respond to the pheromones of bark beetles. Generally, they are attracted to volatiles from their specific trees, but also to α-pinene and ethanol, while some have their own aggregation pheromones. De-barking felled timber prevents nearly all of them from ovipositing in it (Nair, 2007) and, along with irrigation, otherwise controls most phloem-feeding beetles in imported timber (Skarpaas and Økland, 2009).

Widely distributed lamiine beetles in *Monochamus* have a fairly typical life cycle of the superficial type. *Monochamus* spp. (e.g. *M. alternatus, M. carolinensis, M. titillator, M. scutellatus*) are of special interest because they vector the pine wilt nematode *Bursaphelenchus xylophilus* (Togashi, 1990), which is endemic to North America. For this reason they have become important on conifers in South-East Asia and Japan (Shoda-Kagaya, 2007). As with bark beetles, trees under physical stress, nematode attack and/or with depleted resin flows are more susceptible. Small batches of eggs are laid in slits chewed in the bark. Larvae, according to temperature, normally take a few years to develop, feeding between the bark cambium and the sapwood, partially girdling the tree and leading to its further decline. Resin often swamps the young stages. After a final instar in the sapwood, the larva pupates in a chamber immediately under the bark, often in complex cocoons therein. Here, specialized larval forms of the wilt nematode, which have been living in the xylem tissue, enter the spiracles of young adult beetles in their thousands. Pre-reproductive adults fly to the tree-tops, feed on various tissues richer in nutrients than those on the boles, and mature their reproductive tissues, a behaviour reminiscent of that in young cockchafers (Section **3.2.1.2(b)**). They continue to distribute the nematode. In northern Honshu, interesting studies using microsatellite markers reveal that *M. alternatus* has an ambit of redistribution of only a few kilometres, populations to the east and west of the Ohu Mountains being distinct genetically (Shoda-Kagaya, 2007). Several other conifers including fir, cedar and larch are susceptible to these beetles, while spruce is apparently tolerant. Because the larvae are long lived they are easily spread in exported timber. Recent European Union legislation requires that coniferous timber be heat treated before importation.

Monochamus notatus attacks pine and fir trees in the New England states and since the adults may be ~30 mm long, it can do considerable damage. As its name suggests, *M. oregonensis* is found on the Pacific Coast and affects firs, while *M. titillator, M. scutellatus* and *M. maculosus* attack pines in southern states. *Monochamus urussovii* is found in Poland. The lamiine beetle, *Oberea bimaculata,* can be a nasty pest of blackberry and raspberry canes, which the larvae bore. *Goes tesselatus* bores and often destroys oak saplings. *Saperda* (Lamiinae) contains several important pests of first the sapwood and then the heartwood of forest and orchard trees. Young larvae can girdle a tree, older ones weaken it structurally. *Saperda candida,* which is disruptively patterned with white vittae, attacks apple, on which it was formerly a major pest, and other trees in the Rosaceae, *S. calcarata* bores poplars and willows, *S. vestita* linden and *S. tridentata* elm. *Megacyllene* (= *Cyllene*) *caryae* is the painted hickory borer. Females oviposit in spring in the bark of this valuable tree, whose wood makes good shafts for implements. *Monochamus robiniae* bores healthy locust trees, *Glycobius speciosus* attacks sugar maple, *Semanotus litigiosus* tunnels into fir trees, *Canonura princeps* affects Ponderosa pine, *Dirphya nigricornis* bores coffee branches, while *Prionus laticollis* bores tree roots.

In western USA, several species of *Desmocerus* (Lepturinae) are notable because the adults are sexually dimorphic, the males having scarlet elytra while those of the females are dark green. They feed on elderberry. The population dynamics of *Saperda* and *Oberea* have been investigated by Grimble and Knight (1970, 1971) and of *Monochamus* by Togashi (1990). For *O. schaumii*, desiccation and inviability of the eggs were significant but later in development parasitism from the braconid wasp *Cenocoelius sanguineiventris* and several ichneumons, particularly *Cremastus nordi*, occurred. In California, and originally in Australia, two *Phoracantha* beetles attack imported *Eucalyptus*, but *P. recurva* is replacing *P. semipunctata*, whose contemporary decline may be due to its poor defences against a common encyrtid egg parasitoid *Aventianella longoi* (Reitz and Trumble, 2002), a probable case of trans-specific mortality (Section **10.2.3.9**). This parasitoid, which is used in biocontrol, has different strains with different host preferences (Wang, Q. *et al.*, 2008).

Several species attack tropical hardwoods, including *Hoplocerambyx spinicornis*, an important pest of *Shorea* spp. trees from India to Malaysia. In the 1994–1999 outbreak in Madhya Pradesh, 3 million of these trees were affected and most of them died (Dey, 2001, in Nair, 2007). Such outbreaks can influence successional changes in tropical forests. In India, *Xylotrechus* spp. attack teak and *Celosterna scabrator* Eucalyptus. In Africa, the highly polyphagous *Omedia gahani* attacks 127 genera in 56 families (Jones and Curry, 1964, in Gray, 1972). But several tropical cerambycid beetles, such as *Cryiopalus wallacei*, *Eurysops burgeoni* and *Prosopocera brunneus*, are thought to be oligophagous. There are many cases where adult cerambycid beetles have ultimately emerged from timber made into furniture. In this connection, some species such as the widely distributed *Hylotrupes bajulus*, found in timber used for construction, can take as long as 10 years to develop.

4.2.1.2(f) COLEOPTERA; Cerambycidae; Other Lamiinae. A specialized group that cuts off small branches. These are generally large beetles in several genera, although not all lamiine beetles have this behaviour. Like twig *Rhynchites* (Section **4.2.1.2(k)**), they lay eggs in terminal sections of branches and then excise them. These pieces, which can be up to 2 m long, drop to the ground, thwarting the development of induced defences (Section **2.4.2**) as larval growth proceeds. In Jamaica, *Steirastoma breve* affects *Ceiba pentandra*, *Bohinia* spp., *Coriaria pulcherrima*, cocoa *Theobroma cacao* and especially *Albizia lebbeck*, their attack being confined to the ends of the rainy seasons. Up to 50 eggs are laid in a branch and ten or more adults emerge, some after 6 months and others after a year (Freeman, unpublished data). This is another case of risk spreading and recalling the 2-, 3- or 4-year period of development in *Oberea* (Grimble and Knight, 1971). But if the branch falls into a dry spot the larvae may desiccate. Also, in Jamaica, a small lamiine species attacks gungo peas. In North America, *Oncideres cingulata*, the twig girdler, attacks a variety of deciduous trees in forests and orchards. Like other pests that kill the terminal stems, they destroy apical dominance and produce misshapen trees.

4.2.1.2(g) COLEOPTERA; Scolytidae, Platypodidae. *Dendroctonus, Hylurgopinus, Ips, Phloeosinus, Scolytus* (~6000 described spp.), *Platypus, Trypodendron, Xyleborus*. Bark beetles, Ambrosia beetles. Most of these beetles infest the large woody trunks and branches of forest or, occasionally, of orchard trees. There are two types of attack, which relate to the two microhabitats that massive woody tissue provides: (i) the scolytid type in which the beetles live under the bark within the living bast, often passing only a single generation there; and (ii) the platypodid type in which they penetrate deeply into the heartwood, usually spending several generations there. Some scolytid genera, such as *Dendroctonus* (meaning *tree destroyer*), are capable of initiating an *en masse* attack on living trees. These are the most important pests. Other species may follow them, or can attack only weakened, old or moribund trees. For example, in calliphorid flies causing 'strike' of livestock (Section **7.4.2.1**), there are primary and secondary species. Ambrosia beetles, too, usually attack weak trees. In a given geographical region, one or two scolytid species often affect a few species of conifer, but within these favoured species, individual trees vary greatly in their susceptibility (Raffa and Berryman, 1987).

Male bark beetles often construct 'nuptial chambers' and attract one or more females for mating. These females then construct independent brood galleries in which they oviposit in regular notches that they chew along them. In *Dendroctonus* and some other genera, however, it is the females that find a suitable tree (Coulson, 1979). The larvae destroy the sapwood, pupate in chambers beneath the bark and emerge through it, leaving obvious exit holes. These traces make bark beetles good subjects for studies on population dynamics (Beaver, 1966, 1967; Garraway and Freeman, 1981, 1990; Section **11.4.2**). But there are variants from this basic scolytid theme: *Pityophthorus* confines its attention to twigs, *Conophthorus contortae* and *C. lambertianae* attack coniferous cones (Section **6.3.1.1(c)**), *Hylastinus obscurus* is the aberrant clover root scolytid, and species of *Hypothenemus* are found in fruits and even grasses (Section **6.3.1.1(b)**).

While there are fewer species in these two families than in the preceding one, their deleterious effects on forest trees are generally greater. Conifers in northern Eurasia and America are especially affected, but the group also attacks temperate broad-leaved and tropical trees. Indeed, some species have a wide distribution, for example *Ips calligraphus* and *I. grandicollis* are found infesting a variety of pine trees from Honduras and Jamaica to the Canadian border. *Dendroctonus adjunctus* has killed many natural stands of *Pinus rudis* in Guatemala (Gray, 1972), and *D. frontalis,* the southern pine beetle, is found far south into Central America, being the most serious pest of pines in Mexico. But it extends as far north as Wyoming, USA, (44°N). *Dendroctonus ponderosae*

(= *D. monticolae*), the mountain pine beetle, ranges from 31°N to 56°N, and will attack pines at over 2500 m elevation. However, although a great deal of work has been done on the bionomics of this group in temperate situations, especially in North America, much less is known of them in the tropics (Gray, 1972). Beeson (1941), however, made an early survey of their damage in the Indian region, while F.G. Browne worked on them in Malaysia. Garraway (1983) described the destruction of Caribbean pine in Jamaica by *I. calligraphus*, and work is currently underway in Mexico. In addition, *Phloeotribus liminaris* attacks peach trees in warm-temperate areas, while in the tropics *Hypocryphalus mangifera* occurs in mango trees. The evocatively named *Xyleborus fornicatus* bores tea bushes in Sri Lanka, while *X. destruens* destroys young teak in Indonesia.

Ambrosia beetles and probably most of the phloem feeders are associated with fungi, which they transport and eat, that is, there is tritrophism: tree, beetle, and fungus. Dispersing beetles spread fungal spores of *Ceratocystis* and *Europhium* either in their faeces or in a variety of special structures called *mycangia*. These are on the head or prothorax, but microbes such as yeasts and bacteria have also been found. In some species, such as *D. frontalis*, phoretic tarsonemid mites have been implicated in dispersing these pathogens, in this case the blue stain fungus *Ceratocystis minor* (= *Ophiostoma minus*) (Bridges and Moser, 1983). Ambrosia beetles are attracted to dead, fermenting trees by responding to ethanol (Moeck, 1970). They spend much time preparing a suitable medium of wood and faecal particles to propagate fungi. In phloem feeders, fungal inoculation is an integral part of the attack pattern. Fungal mycelia penetrating the ray cells, grow radially and vertically and may terminate the trees resinous defences.

Sex ratios vary widely in these beetles. In polygynous species, the males, who emit an attractive sex pheromone, normally initiate boring. In *Ips* species they may each attract three or four females. Both sexes then produce aggregation pheromones, *cis*- and *trans*-verbenol, often called 'ipsenol'. In *Dendroctonus*, frontalin and seudenol attract largely conspecific males from distances of up to 200 m. Essentially, pheromones increase the size of the target (Section **10.2.4.4**). In most monogynous species the females initiate attack, as in the European *Scolytus scolytus* (= *S. multistriatus*). But in one such species, *Phloeosinus serratus* (= *neotropicus*) that attacks juniper in Jamaica, the males bore in first (Garraway and Freeman, 1981). In ambrosia beetles there are numerous females per male, in one recorded case 60:1, strongly suggesting inbreeding with sibling mating (Hamilton, 1967). Indeed, in *Xyleborus* the males are flightless (Nair, 2007) and haploid (Hamilton, 1996).

In *Dendroctonus*, ovipositing females seem to restrict the number of eggs they lay when their populations under bark are dense, producing a pheromone repellent to potential, conspecific colonists. The anti-aggregation pheromone 3-methyl-2-cyclohexen-1-one has been recognized. Such a mechanism has features congruent with Wynne-Edwards' rather discounted theory of population (Section **11.2.3.1**). In other genera, larval competition for space (Section **9.8**) may ensue, leading to smaller adults and/or greater juvenile mortality. Indeed, mortality patterns are diverse.

Dendroctonus ponderosae normally has considerable resistance to low temperature, the LD_{50} (Section **10.2.3.2**) for the eggs being about −17°C, while that for mature larvae is about −40°C (Logan *et al*., 1995, in Safranyik *et al*., 2010). Although mature larvae are the most temperature-resistant overwintering stage, the adults of this and other bark beetles often overwinter in litter and/or soil. Possibly as a result of global warming, *D. ponderosae* has recently devastated pine stands in central British Columbia, Canada (Safranyik *et al*., 2010). A warm August facilitates flight of the adults and hence spread of the outbreak, while a dry spring stresses the pines for moisture, limiting their defences. Indeed, the beetle's eggs are often killed by contact with resin. On the other hand, a warm year results in partial bivoltinism and maladapted overwintering stages. There are well-founded fears that, due to less cold winters, its destruction could spread east through the boreal pine forests of Canada towards Ontario.

Although >150 species of hymenopteran parasitoids have been recorded from North American bark beetles alone (Bushing, 1965), they are held generally to be of little importance in scolytid population dynamics. This is also true of several other insect groups (Thompson, 1929). Much mortality of bark beetles results from the resistance of trees they attack (Raffa and Berryman, 1987), a *bottom-up* effect (Section **10.1**). Parasitoid females either penetrate the bark with their ovipositors or seek their victims in the privacy of their tunnels. Several braconid species of *Coeloides*, *Dendrosoter*, *Heterospilus* and *Spathius* are involved. For example, *S. canadensis* attacks the beetle genera *Dendroctonus*, *Ips*, *Phloeosinus* and *Scolytus*. Many of these wasps also attack cerambycid beetles: *S. canadensis* is recorded from *Saperda* and also from the buprestid beetle *Agrilus*. Other notable parasitoids are eurytomid (*Eurytoma*), pteromalid (*Cecidostiba, Cheiropachus, Heydenia* and *Tomicobia*) and torymid wasps (*Roptrocerus*). These parasitoids use synomones from trees (*a*-pinine, *a*-cubene) and diverse kairomones (q.v.) from their hosts to locate their victims (Vinson, 1984). In the UK, *Entedon leucogramma* parasitizes *Scolytus scolytus*, but the mortality it causes is possibly inversely density dependent (Beaver, 1967; Section **10.2.3.9**). To appreciate the complexities of such parasitism on bark beetles, see Bushing's (1965) paper and Linit and Stephen (1983) on the enemies of *Dendroctonus frontalis*.

Healthy trees usually have considerable resistance to the attack of most bark beetles (Section **2.4.2**), although some species of *Dendroctonus* and *Scolytus* are exceptionally virulent. Conifers have special canals full of resin, the oleoresin system, in their wood, giving them their 'piny' smell. The resin exudes into wounds made by beetles, gumming up their mouthparts, but also contains defensive compounds (Section **2.4.2**), often monoterpenes (especially limonene), that are lethal or at least harmful to bark beetles and their symbiotic fungi (Raffa and Berryman, 1987, see their Table 1 for details). Should resin flow be reduced as a result of disease, drought, landslide, fire, storms or even mass attack by beetles, more bark beetles quickly colonize the trees (Coulson, 1979). Originally, some workers thought that drought drove the outbreaks of *D. frontalis* (Michaels *et al*., 1986, in Turchin, 2003), and King (1972) had implicated regional rainfall. But a recent sophisticated mathematical investigation of time-series data (Turchin, 2003; Section **11.5.2**) indicates that strong, second-order processes, namely predation by clerid beetles, drives their irregular cycles.

Ips acuminatus contributes to the decline of pine trees in Switzerland (Wermelinger *et al*., 2008). In Scandinavia, widespread damage lasting several years ensued in coniferous forests after localized damage due to storms had caused a build-up of bark beetles (Bakke and Strand, 1981, in Hanski, 1985). The nature of the soil where the trees grow and whether it is susceptible to drought or flooding are other physical factors of importance. In dense forest, shading out by more vigorous trees causes the slower growing ones to die, which may become outbreak foci for the beetles. For example, stressed Douglas fir trees succumb to attack by *Dendroctonus pseudotsugae*, a serious North American pest that can ring bark and kill the tree, while *D. micans*, the giant spruce beetle, can invade healthy trees. In *D. frontalis* the concentrated attack of several thousand beetles, congregating in response to a pheromone, overcomes the defences of a healthy pine tree. Similarly, in *D. brevicornis*, an important pest of Californian conifers, there are frequent *en masse* attacks, using the pheromone *exo*-brevicomin produced by successful females and then frontalin by the immigrant males. But very high densities are avoided by the production of two more pheromones, *trans*-verbenol and verbenone, produced by the residents (Byers, 1992). It would seem that the beetles adjust their population density to that favourable for the constituent individuals. Generally, the overall incidence of attack in stands is a function of the number of potentially colonizing beetles and the density of susceptible trees.

Dendroctonus micans is probably capable of resisting resin by reason of its large size and also because of the peculiar communal feeding behaviour of the larvae. Trees produce a battery of other organics, including phenols and tannins, in their defence against beetle attack (Section **2.4.2**). Tannins bind with carbohydrates and proteins, making them less digestible. Some fir trees possess a compound that mimics juvenile hormone, and this delays or prevents insect metamorphosis. Berryman (1986) found that *D. ponderosae,* which regularly devastates old stands of lodgepole pines in western North America, are deterred by those having a high density of resin canals, an example of variation between trees (Section **2.4.2**). As in *D. frontalis*, females colonizing a given tree attract others by emitting a congregation pheromone. Some species of this genus leave the trees after laying some eggs and may infest other trees. In several genera the flight muscles regress during reproduction (Atkins and Farris, 1962), but as in *Apion* (Freeman, 1967a), they may redevelop.

Long-lived conifers like yews and redwoods are almost unaffected by insect pests in general, and especially by bark beetles. They are thought, therefore, to have effective defences. Others, like several of the pines, are short lived. One such example is the Ponderosa pine of North America, which is attacked by at least 23 species of bark beetles and 43 browsers. The infestation of trees often follows one of the forms of stress listed above. But when forest plantations are thinned a large amount of small branch material (slash) is left behind. Beetles may breed in this if the branches are large enough, and their numbers increase, particularly if the operation is providing freshly cut material over a lengthy period, so that the beetles can pass through several generations in the same locality. Beetles will infest cut logs and felled trees if given the slightest opportunity. Indeed, their biology and dynamics are often studied by placing sample logs in the field (Beaver, 1966; Garraway and Freeman, 1983, 1990). Recall that de-barking is practised to circumvent such insects attacking felled timber.

Bark beetles often attack a specific size range of the trunk, which relates to the depth of the bast in which they breed. For example, *Dendroctonus frontalis* are attracted to the vertical shape of the bole and breed in the mid-sections of big trees, while *D. ponderosae* also require large trees with thick phloem. In fact, in small trees the population rate of change is negative (Turchin, 2003), namely a *sink patch* (Section **12.2.4.2**). But *Ips pini* prefer small trees or the tops of large ones. *Tomicus piniperda* prefer the boles of Scots pine (Schroeder, 1996).

Scolytus scolytus carries the infamous Dutch elm disease. In about 1975, this beetle started a plague in England that resulted in the death of almost all mature elm trees. The aesthetic loss to the countryside is immeasurable. Similarly, this beetle and the native *Hylurgopinus opaculatus* have caused the near extinction of American elms in the mid-western USA. These beetles carry the ascomycete fungus *Ceratocystis ulmi,* whose hyphae spread in the tree's xylem and phloem, blocking its transport system. English elms persist by virtue of their reproduction by suckers, although occasional isolated trees can still be found; a nostalgic sight! Now when the trunks of young elms reach a diameter of ~8 cm, the minimum size for attack, invariably they become infested and die within a few years (Fig. 4.2). But it is interesting that small elm trees now seem to have a greater prevalence in English hedgerows than before. In North America, *Dendroctonus ponderosae* infects *Pinus contorta* and some other pines with the fungi *Grosmannia clavigera* and *Ophiostoma montium*, while *Scolytus ventralis* infects *Abies grandis* with *Trichosporium symbioticum*. *Pityophthorus setosus* and *P. carmeli* transmit the fungal pathogen *Fusarium circinatum*, causing pitch canker of Monterey and other pines and some firs. This disease may be carried by some *Ips* and *Conophthorus* species (Section **6.3.1.1(c)**).

Dendroctonus micans (above), is one of the few cases in which biological control of a bark beetle has been effective. Here, the beetle *Rhizophagus grandis* (Section **8.2.2.4(e)**) lays egg batches where it detects the presence of *D. micans,* the communal habits of its prey making them vulnerable to its predatory larvae. In the southern USA, the clerid beetle *Thanasimus dubius* is a major predator of *D. frontalis.* It is attracted to their aggregation pheromone, showing an aggregative response, and may kill up to 60% of adults before they can enter a tree (Reeve, 1997). Its larvae also eat those of the bark beetle, there being evidence of density-dependent predation (Section **10.2.3.9**). Adults emerge 1, 1.5 or 2 years later, thus spreading risk (den Boer, 1968). Even so, this bark beetle has recently caused great damage to pines (*Pinus taeda, P. echinata*) in this region. In the Rocky Mountains, *Th. undatulus* is attracted to the aggregation pheromone of *D. pseudotsugae* (Ross and Wallin, 2008). In Eurasia, *Th. formicarius* eats *Ips typographus* in spruce trees and *Tomicus piniperda* in Scots pines. In Sweden, both *Th. formicarius* and *Rh. depressus* attack *T. piniperda*, although it lacks an aggregation pheromone (Schroeder, 1996). These predators respond to pine tree volatiles, but there is a strongly negative interaction between them. In addition, larvae of the dolichopodid fly *Medetera aldrichii* often feed on bark beetle larvae. Recent research on European scolytid beetles is covered in Lieutier *et al.* (2004).

4.2.1.2(h) COLEOPTERA; Curculionidae. *Pissodes strobe*. White pine weevil. A North American pest of young (~10–15 year) pines and spruces. This is a notorious pest of young trees. The larvae mine the terminal shoots, destroying apical dominance and frequently produce a forked tree instead of a straight one, reducing its commercial value. Where forests are clear felled (i.e. all the trees are cut down in one operation) and then replanted, their depredations may be serious (Overhulser *et al.*, 1972), especially when soil conditions are poor. These include bad drainage and subsequent water logging, but also excessive dryness. This pest is far less common where the forest canopy is maintained or where mixed stands of other trees are grown (Graham, 1915, 1926, in Pimentel, 1961). *Pissodes approximatus* and *P. terminalis* are similar species, the latter destroying lodgepole pines.

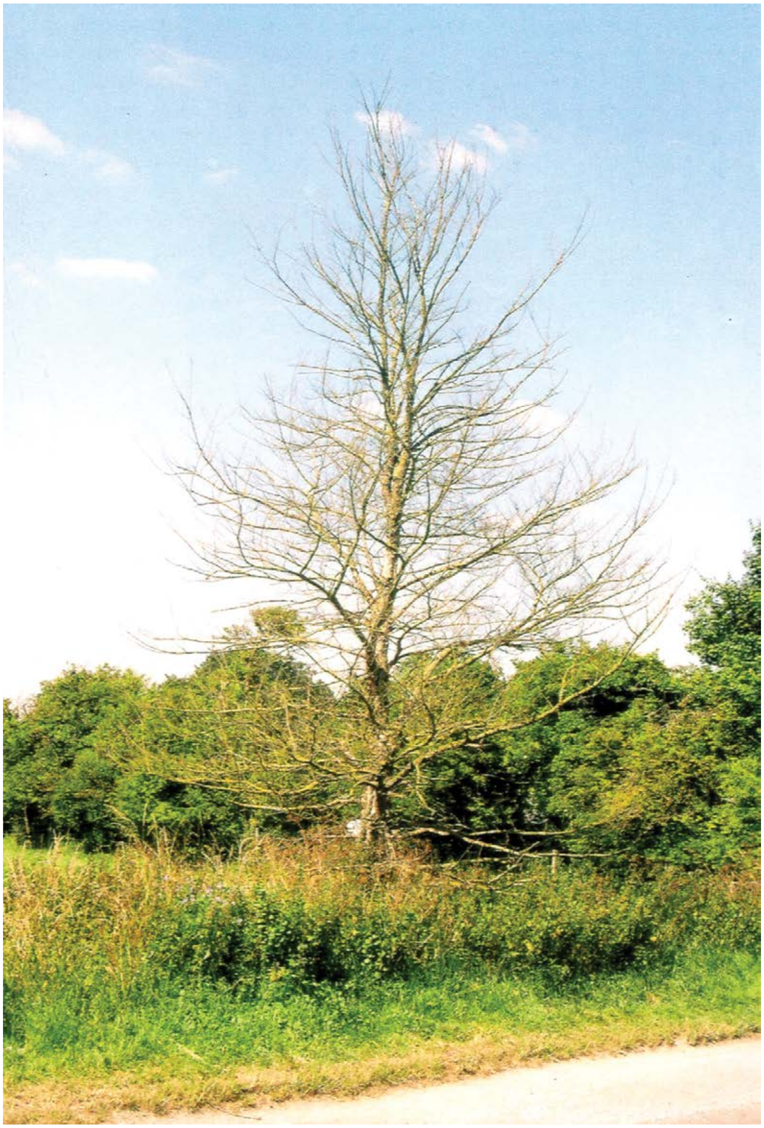

Fig. 4.2. Young elm trees killed by *Ceratocystis*, a fungus transmitted by the bark beetle *Scolytus* (Scolytidae).

4.2.1.2(i) COLEOPTERA; Curculionidae. *Hylobius* spp. Root collar weevils. Temperate pests of saplings. These beetles breed in the stumps of freshly cut forest trees in eastern North America and Northern Europe. Two North American species are *H. pales* and *H. radicis*. The emerging adults attack the bark of newly planted saplings and are, therefore, of particular importance after clear felling. *Hylobius abietus* may fly 'several tens of kilometres' locating recently killed conifers, the preferred breeding medium (Solbreck, 1985, in Pedgley *et al*., 1995). In North America, *H. radicis* breeds preferentially in *Pinus resinosus* saplings when they are 10–13 years old, causing them to die or to fall under windy conditions. Vigilance is therefore necessary when they approach this age. It also infests *P. sylvestris* grown for Christmas trees, providing reservoir populations (Section **13.1.2.2**). These should be planted several kilometres from *P. resinosus* plantations (Kennedy and Wilson, 1971).

4.2.1.2(j) COLEOPTERA; Curculionidae. *Rhynchites caerulius*. Apple twig cutter. A temperate pest of apple. These small weevils lay eggs in spring in the terminal twigs of apple trees. Then they bore a ring of punctures around the twig, so thwarting the tree's defences. Development takes place in this apical segment, which eventually dies. Then, the plants shoot out laterally below the dead twig, spoiling their shape and reducing production. The weevil *Alcidodes brevirostris* does similar damage to African cotton.

4.2.1.2(k) COLEOPTERA; Curculionidae. *Rhynchophorus* spp. Palm weevils. There are two important species, *R. ferrugineus* that have been affecting palms for some time in the Middle East and the Mediterranean, whereas *R. vulneratus,* a polymorphic black and red species, has only recently turned up in California where its boring larvae are busy killing iconic palms (Cranston, 2018). Where these trees are a public amenity they must be removed before they fall, entailing considerable cost. Data palms are also affected. Finally, an all-black species, *R. palmarum*, has invaded California from Mexico. Apart from killing palms directly it also vectors a pathogenic nematode causing red-ring disease of palms. These weevils have been locally eradicated using bucket traps of fermenting dates and pineapple together with a *Rhynchophorus* pheromone.

4.2.1.2(l) HYMENOPTERA; SYMPHYTA; Siricidae. *Sirex* (= *Urocerus*) *gigas, S. noctilio, S. cyaneus, S. juvencus, Xeris spectrum, Tremex* spp. Horntails or wood wasps. Timber pests, generally in northern coniferous forests. These large, structurally primitive wasps lack the fine waist found in higher Hymenoptera. Instead they have a prominent, rigid ovipositor. *Pseudosirex*, an extinct relative of *Sirex*, dates from the Upper Jurassic. *Sirex* spp. have different methods of boring, with single or multiple drill holes. Generally, several eggs are inserted into the bark of living, weakened, felled or fallen trees, mainly pines. Adult life span is normally <2 weeks. The larvae bore the wood, being dependent on the basidiomycete fungus *Amylostereum areolatum* and sometimes *A. chailletii* (Stereaceae) whose ligno-cellulotic enzymes cause breakdown of the xylem (Sarvary *et al.*, 2016). A fungal inoculum is carried in paired mycangia near the ovipositor (Spradbery, 1977). The metallic blue *S. noctilio*, originally Eurasian, arrived in North America early this century, and previously in Australasia, South Africa and South America (Corley *et al.*, 2007). Females also inject a phytotoxic mucous (Foelker, 2016) which causes phytotoxic symptoms and kills pines. But their spread may be reduced by indirect competition with several bark beetles (Section **4.2.1.2(g)**), since the fungi they vector, such as *Leptographium* and *Ophiostoma* (Ophiostomataceae) limit the growth of *A. areolatum* (Ryan *et al.*, 2011). Poor growth of this symbiont reduces the reproductive success of this wasp. *Xeris spectrum* is a secondary species, lacking fungal symbionts. In the taiga, stacked logs may be infested by horntails in the summer months, allowing other fungi and bacteria to penetrate more rapidly and causing degradation of the timber, as happens in the normal soil formation (Section **8.2.4**).

On felled timber, de-barking and/or a superficial spraying with a long-lasting, tenacious insecticide can provide protection, or logs can be covered in black plastic and exposed to the sun to 'cook' the larvae. Several ichneumons (*Megarhyssa, Rhyssa*) and the cynipoid wasp *Ibalia* are associated with *Sirex* (Section **8.2.2.5(l)**), the former causing density-dependent parasitism on *S. noctilio* (Foelker, 2016). In New York State, *Megarhyssa nortoni*, *Rhyssa lineolata, R. persuasoria, R. crevieri* and *Ibalia leucospoides* have been recorded (Long *et al.*, 2009). The nematode *Beddingia siricidicola* has been used as a biocontrol agent. *Sirex noctilio* is a contributory cause of the slow decline of *P. sylvestris* trees in Switzerland (Wermelinger *et al.*, 2008). *Sirex gigas* has been reported from Australia and New Zealand, which it presumably reached in exported timber. *Sirex nigricornis* and *S. edwardsii* are recorded from North American pines. *Tremex* affects deciduous trees there but it is seldom a pest. Its ichneumonid parasitoid *Thalessa* wealds an ovipositor ~12 cm long.

4.2.1.2(m) LEPIDOPTERA; Cossoidea, Cossidae. *Cossus*, *Xyleutes* and *Zeuzera,* some other cossid genera. Goat and leopard moths. Cosmopolitan pests of branches in orchards and of some forest trees. The cossid moths comprise ~110 genera and ~700 species (Degefu *et al.*, 2013). Two main ecological features affecting attack are that adults have good dispersive powers and that larvae are long lived. Long development is a characteristic of pests like these that live in heartwood (Hamilton, 1996). It takes 2–3 years in temperate *Cossus* and *Zeuzera*, but 1 or 2 years in tropical *Xyleutes*. Pupation in the leopard moth occurs immediately under the bark, which the larva chews, allowing the jawless adult to escape subsequently, but saw-like teeth on the pupa assist this. Goat moth larvae, however, often leave their burrow and pupate in the soil or other debris, hence reducing their population density. In this group the females are much larger than the males, suggesting that there has been strong selection for high fecundity and/or investment by females (Section **10.2.5.1**). Indeed, in *Xyleutes ceramicus* achieved fecundity (AF) is estimated at 12,500 (Gotoh *et al*., 2002, in Nair, 2007), and, like winter moths, the young larvae migrate on silken threads.

In temperate regions, *Z. pyrina* attacks top fruits such as apples, pears, plums and cherries, as well as a variety of forest trees. Originally European, it got into North America in about 1882. In Mediterranean regions it affects apricots, peaches and citrus. Young larvae bore the smaller twigs and later move to the large branches or the trunk. Damage becomes apparent after the fall: the bored and weakened limb of a tree fails under the weight of the developing fruit, generally during rain or high winds. Specific insecticidal control is not feasible, so it is fortunate that the intensity of attack is generally low. Recently, however, control using a sex pheromone has been used to disrupt mating. *Zeuzera coffeae* attacks coffee, tea and *Acacia* in Asia.

Xyleutes ceramicus and *Alcterogystia* (= *Cossus*) *cadambae* are major pests of teak trees in parts of India and South-East Asia (Gray, 1972; Mathew, 1990, in Nair, 2007). Although *Xyleutes* tunnels into the heartwood for ~25 cm, it feeds on callus tissue under the bark, but since it does not kill the tree these borings, which act as refuges for pupation, accumulate as the tree grows, greatly reducing the value of the timber. Its distribution and population density are affected by rainfall, causing major damage only between 1750 mm and 2750 mm mean annual precipitation (Beeson, 1941). *Alcterogystia cadambae* is confined to India and unlike *X. ceramicus* may kill older trees. *Coryphodema tristis* in South Africa and *Chilecomadia valdiviana* in Chile have recently become pests of *Eucalyptus nitens* plantations (Degefu *et al*., 2013). The North American carpenter larvae of *Prionoxystus macmurtrei, P. robiniae* and *Cossula magnifica*, are other cossid pests.

4.2.1.2(n) LEPIDOPTERA; Sesiidae (= Aegeriidae).

Synanthedon exitiosa. Peach tree borer. Clear wing moths. A ubiquitous pest of peach trees in the USA. This family is probably related to the Cossidae and contains many day-flying species that mimic wasps and bees, and visit flowers. Several of their names such as '*apiformis*', '*bembeciformis*' and '*vespiformis*' attest to this similarity. The larvae bore in wood, while the pupae, like cossid species, have special spines to assist their escape from these confines. Apart from the species given below, they are of minor economic importance.

Adult *S. exitiosa*, unlike most sesiid moths, show a strong sexual dimorphism, males having both wings almost entirely devoid of scales, whereas females have completely scaled forewings. Otherwise they are steely-blue in colour. They oviposit near the base of the bole of peach trees and the larvae bore into the wood, passing below soil level in the winter. Their presence can be discovered from the gummy secretions of the attacked trees. Mature larvae pupate in the soil in spring and adults may be found throughout the summer, leading to an extended period of oviposition. Trees weakened at the base by the boring activity may snap in a high wind.

Synanthedon opalescens, which occurs on the Pacific Coast of North America, is also a pest of peach trees, while *S. pictipes* bores plum, cherry and some other trees in addition to peach, and can be important in the eastern USA. *Synanthedon* (= *Aegeria*) *myopaeformis* occasionally attacks apple, *S. hector* cherry, *S.* (= *Chamaesphecia,* = *Aegeria*) *tipuliformis* and *Bembecia marginata* affect red and black currants and raspberry canes, respectively. They are also found in Europe. Rather atypically, *S. bibionipennis* larvae bore the crowns of commercial strawberries along the Pacific Coast, but also attack commercial *Rubus* cultivars. Heavy infestations can destroy a field in a single year (Bruck *et al*., 2008). By contrast, *S. sequoiae* bores giant redwood trees. *Synanthedon scitula*, the dogwood borer, is a pest of apple trees, but also affects ornamental shrubs in eastern USA (Bergh *et al*., 2009). *Vitacea polistiformis* attacks American grapes, but mainly affects the root system. Pheromones disrupting mating and improving the timing of spraying, often with chlorpyrifos, have been used against these moths. In *S. scitula,* the sex pheromone is a blend of three complex compounds in specific proportions. Experimental work with a variety of entomopathogenic nematodes, including *Steinernema*, *Heterorhabditis* and *Neoaplectana*

(Section **13.2.4.5**), continues on *S. bibionipennis* and other sesiid borers (Arthurs *et al*., 2004). These agents destroy the burrowing larvae where insecticides cannot reach them.

4.2.1.2(o) LEPIDOPTERA: Pyralidae. *Hypsipyla grandella*, *H. robusta*. Respectively Neotropical and South-East Asian borers of teak, mahogany and related Meliaceae, affecting young shoots. The Pyralidae contain several serious and many more less serious pests. Both the above species are large for pyralid moths, having a wingspan of up to 50 mm. The females are the larger, as in several other wood-boring moths. Eggs are laid singly on shoots during the rainy season, but in *H. grandella* several eggs may be laid. In *H. robusta,* AF may be >500 (Speight and Wylie, 2001), rather less in *H. grandella*. The larval period is ~3 weeks, much shorter than that in borers of mature wood, and the large larvae are peculiarly bluish with rows of black spots. They block the tunnel with a mass of frass bound with silk, but may seek a second shoot if the natal one provides insufficient food. Since the pupal period is <2 weeks, there are several generations/year under wet tropical conditions. In the north of India, however, mature larvae diapause within the shoots in the cool winter months, and here *H. robusta* attacks both the shoots and fruits of toon trees (*Toona ciliata*). But both this tree and *Khaya ivorensis* (Meliaceae) resist attacks by *H. grandella* in Latin America (Gray, 1972).

Shoot boring is especially destructive in sunny conditions, affecting young mahogany and West Indian cedar, *Cedrela odorata*, both of which are valuable for timber. Shoots are more vigorous in the open, are thought to provide superior food, and selectivity by ovipositing females indicated. Attacks are less frequent on older trees. When terminal shoots are bored, saplings may die. Later on, apical dominance is lost and side shoots develop, which may be bored subsequently. Larvae also bore flowers and fruits (Gray, 1972). They are atypical borers of trees, attacking before lignification is complete. They are more frequent in teak plantations, but using shade trees and under-planting should prove effective in reducing damage (Nair, 2007). Fungi (*Beauveria bassiana* and *Cordyceps* spp.) cause significant mortality under humid conditions. Howard (1995) found that treatment with azadirachtin, an extract from neem trees, reduced boring significantly.

Along the Mediterranean coasts of France and Italy, another large moth (~100 mm wingspan) with boring larvae, *Paysandisia archon* (Castniidae), has recently caused great damage to various ornamental palms. Originally from Uruguay and Northern Argentina, it came to the Mediterranean in imported decorative palms, another case of ignorance in action. The diurnal females lay large (5 mm) eggs in the young leaf bases and the larvae bore these and later the trunks. Mature larvae have swollen thoracic segments like buprestid beetles and may reach a length of 7 cm. Various other stem-boring moths affect pines. *Eucosma gloriola* and *E. sonomana* (Eucosmidae) bore terminal shoots of jack pines (Price, P.W., 1997), and *Dioryctria albovitella* (Pyralidae) attacks shoots and cones of *Pinus edulis*. Numbers of *Evetria* (= *Rhyacionia*) *buoliana* (Olethreutidae), which periodically damages Scots pine shoots in Western Europe and North America, are depressed by high levels of resin in the buds, but survive better during warm summers. Its eulophid parasitoid *Hyssopus thymus* often attacks it in eastern Canada. Several other similar species of *Evetria* exist.

4.3 Sucking Pests of Woody Stems

These bugs belong to a few homopteroid families, and affect only living wood where secondary thickening is proceeding, while their relatives often attack soft annual stems (Section **4.5**). We have already dealt with cicadas in the previous chapter, since the damage they cause is due mainly to nymphs within the soil. The adults, however, that fly for a few weeks at the height of summer, may be sufficiently numerous to cause some damage to decorative shrubs by sucking their branches and ovipositing in the twigs. Sucking pests generally connect into the plant's phloem, but a few such as the cicadas, cercopid and cicadellid bugs feed from the xylem. We noted above that homopteroids show an increasing association with their plant food. Apart from the primitive cicadas being large and the structurally advanced families in the Sternorrhyncha (whiteflies, aphids, coccids) being small, there are also increasing complexities in their life histories. These include alary polymorphism, alternation of generations, parthenogenesis and the development of very high fecundities in some coccid bugs.

4.3.1.1(a) AUCHENORRHYNCHA; Membracidae. Tree-hoppers. Membracid bugs are recognized by the large and often ornate extension of the pronotum, which may reach back as far as the end of the abdomen (Borror *et al*., 1989). The function of these structures is still debated, but they may serve in defence against small predators and in the distribution of sex pheromones. In *Umbonia crassicornis* adults often mass together along a stem, giving the impression of a densely thorny structure. Reproduction is generally straightforwardly sexual, with often only one or two generations/year in temperate regions. Some species, however, show parental care (Hinton, 1977; Wood, 1993). Females in several groups guard the eggs from potential predators, less well against parasitoids. There are also mutualistic interactions with ants, and in some cases females will not lay eggs in their absence. Aggregations of egg masses which oddly may involve more than one membracid species, occur frequently. They hatch to give groups of nymphs that are attended by ants. Such sub-social groups and associations with ants are more frequent in the Neotropics than in North America, where numerous solitary membracid species are known. In contrast to aphids, Old and New World membracid faunas are almost entirely distinct, indicating that they lack the aphid's ability for long-distance migration. Caribbean species, for example, are 90% endemic (Wood, 1993). Described membracid bugs are largely tropical species, a situation that will become more marked with further collecting, and there are more species per genus close to the equator and in the 35–45°N zone (Wood and Olmstead, 1984).

These bugs, which are typically monophagous, rarely cause serious damage. Several temperate species associate with oak and in North America ovipositing *Stictocephala bubalus* slit the twigs of top fruits. This is similar to some of the damage caused by cicadas (above), and may result in the death of the twig and loss of apical dominance. In spring, surviving nymphs drop to the herbage beneath the trees where they complete development.

4.3.1.1(b) STERNORRHYNCHA; Aphididae, Eriosominae.

Eriosoma lanigerum. Woolly aphid. A pest of apple and pear trees wherever they are grown. Aphids often use woody stems as a winter safe haven, but this pest attacks them during the height of the growing season. It is related to *Pemphigus,* the lettuce root aphid (Section **3.3.3.1(a)**) and often found on old, untended apple trees where successive generations of apterae over several years produce large galls on the branches, termed *perennial canker* (Fig. 4.3). Infestation also occurs on young twigs, which then rapidly become distorted, growing around the point of attack so as to enclose it. While we have placed this species as a pest of stems (because such damage is readily visible), *Eriosoma* like *Pemphigus* also affects roots, where it may produce large nodules. Both forms of attack, of course, reduce production according to their extent.

Fig. 4.3. Perennial canker caused by the eriosomine woolly aphid *Eriosoma lanigerum* on an apple branch.

This pest is also found on pear, hawthorn and mountain ash, but sexual females may lay single eggs in autumn on elm. So there is a wild reservoir of population (Section **13.1.2.2**). In the USA, the eulophid parasitoid *Aphelinus mali* has been employed as a biocontrol agent. Woolly aphid attacks were originally guarded against by 'winter washes', generally of petroleum oils. These killed everything except the eggs of red spider mites, leading to huge increases in their numbers, but have now been replaced by more selective agents (Section **13.3.3.2**).

Related species include *Eriosoma pyricola*, which attacks pear trees, and the woolly elm aphid *E. americanum*. *Longistigma caryae* is the giant bark aphid of eastern USA. It is 6 mm in length when mature and feeds externally on deciduous trees such as hickory and sycamore. Its large size probably means that the mouthparts are long and strong enough to reach the living tissue through the bark. *Stomaphis quercus*, which attacks European oaks in a similar manner, also has long mouthparts. Similarly, *Lachnus roboris,* which also feeds on oak, reaches 4.5 mm in length. In autumn, the oviparae coat the twigs with a mat of closely spaced eggs. *Tuberolachnus salignus* attacks willows, particularly those grown in short rotation for biomass production, but sexual forms have not been found and their method of overwintering is unknown.

4.3.1.1(c) STERNORRHYNCHA; Adelgidae. *Adelges* (= *Chermes*) *abietis*. Eastern spruce gall adelgid. A pest of spruce in northern Europe and north-eastern North America. Some other adelgid pests. Adelgid bugs are confined to conifers, but often several genera are attacked by the same species. Where there is a sexual generation it is normally on spruce. This species is parthenogenetic, at least in North America. It has two annual generations, the winter is passed as immature, diapausing nymphs on spruce buds. In April and May, they mature as apterous females and lay eggs *in situ*. Their feeding induces galls having all the appearance of small green pineapples (Fig. 4.4), in which nymphs of the second generation develop. In summer, winged females emerge from the galls and disperse to adjacent branches and trees, laying eggs on the terminal shoots. In Europe, these migrants may fly to other conifers, including larch, on which the life cycle is different and includes sexual forms. Then there are parallel cycles on different conifers in the second year. We may view such complexity in view of den Boer's theory of risk spreading (Section **9.7**). Some adelgid species have life cycles of even greater intricacy, a veritable tangled skein. *Adelges piceae* is the woolly adelgid of balsam fir. *Adelges tsugae* has killed many *Tsuga canadensis* trees in north-eastern North America (McClure, 1991). Chemical control is ineffective, but the Japanese coccinellid beetle, *Pseudoscymnus*, has been released to combat this insect. *Adelges* is interesting as it has spread from Asia despite the lack of alternative hosts, probably *Picea* spp. Migratory sexuparae are produced in a strongly density-dependent manner (Section **10.2.3.7**), but all perish.

Fig. 4.4. 'Pineapple' galls of *Adelges* (Adelgidae) containing nymphs. Source: Wikimedia Commons, author Sandy Rae.

4.3.1.1(d) STERNORRHYNCHA; Coccoidea. Scale insects and mealy bugs. Scale insects are generally characterized by the sedentary habit of the adult females, the frequent absence of males and a high AF. Even so, their rates of population increase are typically lower than those of aphids, and possibly for this reason, enemies more readily suppress them. Even so, this group was one of the first to show resistance to chemical control (Ripper, 1944). Eggs are normally deposited in a mass under the scale and the young nymphs disperse distally and/or may be windblown. The four families containing important pests are the Margarodidae, Diaspididae, Pseudococcidae and Coccidae. In California, nearly 100 coccoid spp. may need management (see **Chapter 6** for those species that mainly attack fruits). Some mealy bugs, such as the African species *Ferrisia virgata*, are covered with sticky needle-like structures that may deter parasitoids (Pijls and van Alphen, 1996). Members of this family have been shown to contain the endosymbiotic bacterium *Tremblaya princeps*, which assist in their nutrition (Baumann, 2005).

4.3.1.1(e) STERNORRHYNCHA; Coccoidea; Margarodidae. *Icerya purchasi*. Cottony cushion scale. A largely tropical, broad-spectrum pest. This pantropical and Mediterranean scale is very distinctive, being covered by a relatively thick, fluted coat of waxy material giving it the look of a small, white scallop shell (Fig. 4.5). Individuals are peculiar in being self-fertilizing hermaphrodites. For their dynamics this means that all adults lay eggs, not just true females, hence doubling the reproductive potential of the population. It also means that females do not have to wait to be fertilized. Since insects may suffer high daily rates of attrition, such a time-saving strategy is important in increasing reproductive output. Masses of up to 1000 eggs are laid, which are also covered in wax.

Icerya purchasi is most famously the scourge of Californian citrus, but equally famously, successfully controlled by the Australian vedalia beetle *Rodolia cardinalis* (Coccinellidae). However, it

Fig. 4.5. The margarodid scale *Icerya purchasi,* a pantropical pest mainly of soft stems.

appears that the chryptochetid fly *Cryptocheta iceryae*, also introduced from Australia for the same purpose, has a supplementary effect, being more important as a biocontrol agent in coastal areas, while *Rodolia* is more effective inland, probably because of differences in the physical environment that influence the interactions. When DDT became widely used, the vedalia was decimated and adjustments had to be made (Stern *et al*., 1959). Cottony cushion scales are also found on a variety of ornamental shrubs, causing dieback, and under the leaf sheaths of sugar cane, where they cause little obvious damage.

4.3.1.1(f) STERNORRHYNCHA; Coccoidea; Diaspididae. *Quadraspidiotus* (= *Aspidiotus*) *perniciosus*. San Jose scale. A widespread and broad-spectrum pest of fruit trees. Diaspidid or armoured scales are so called because they retain the nymphal exuviae combined with wax as a hard dorsal shield. So a mature female has a stack of three of them on her back. This scale is found throughout the USA and bordering Canada, having been introduced from the Orient about 1880 (Comstock, 1940) into southern California. During World War II it spread into Europe and Australasia. It attacks a wide variety of fruit trees and ornamentals, and severe infestations encrusting the branches can kill the plant. Adult females are oval and some 2 mm in length. Adult males are smaller, without scales and have a single pair of wings. Like aphids may be, this species is viviparous. As is usual in scale insects, the yellow, mite-like first instar nymphs crawl distally on the branches and may spread the infection to leaves and fruits. There are two annual generations in the north and six in the south of its distribution. The species overwinters as partly grown nymphs.

Parlatoria oleae is a bivoltine pest of olives in California, where it is controlled by the aphelinine parasitoids *Aphytis paramaculicornis* (= *maculicornis*) and *Coccophagoides utilis* (Rochat and Gutierrez, 2001). The former wasp is more effective during September to March, while the latter dominates during the summer generation (Luck *et al*., 1988). *Lepidosaphes ulmi* attacks broad-leaved trees in temperate forests and exists in both parthenogenetic and sexual forms. Like *Quadraspidiotus pyri,* it also attacks orchard fruit trees.

4.3.1.1(g) STERNORRHYNCHA; Coccoidea, Pseudococcidae. *Phenacoccus manihoti*. Cassava mealy bug, mealy bugs. Mealy bugs comprise ~2000 described species. Most reproduce sexually and lay eggs although some are parthenogenetic (Resh and Cardé, 2003). Cassava is a South American shrub whose roots may be boiled like potatoes or ground into coarse flour. In that continent, *Phenacoccus manihoti* together with *P. herreni* occur on this crop, but normally at low densities. When introduced into Africa in the sixteenth century, cassava became a staple for some 200 million people and was relatively untroubled by pest insects until the early 1970s. Then *P. manihoti* found its way from its original home and spread rapidly to affect most of the African cassava belt, which is roughly from 15°N to 20°S. Heavy infestations on young stems may be >30,000 individuals per bush (Fig. 4.6), and while not affecting tubers directly, halve their production and impair their quality. This pest provides a recent case of successful biocontrol. In 1981, the South American encyrtid parasitoid *Apoanagyrus* (= *Epidinocarsis*) *lopezi*, (Section **8.2.2.5(p)**) was released in Nigeria (Section **13.2.4.6**). Apart from the spectacular decrease in the pest it affected, this shows the rapid rate at which a minute parasitoid can travel.

Phenacoccus madeirensis is widespread in South America but unimportant on cassava. Two other mealy bugs, *Pseudococcus calceolariae* and *Planococcus citri* attack citrus, *Pl. kenyae* is a pest of Kenyan coffee, and in West Africa *Pl. njalensis* vectors the viral disease of cacao causing ‘swollen shoot’. The eriococcine beech scale, *Cryptococcus fagisuga*, may also be of importance in temperate regions (Berryman, 1986).

Fig. 4.6. An infestation of cassava mealy bugs *Phenacoccus manihoti* (Pseudococcidae). The predators are *Hyperaspis, Exochomus* and *Diomus* (Coccinellidae).

4.3.1.1(h) STERNORRHYNCHA; Coccoidea, Coccidae. *Saissetia oleae*. Black scale; soft, tortoise and wax scales. A Mediterranean and sub-tropical pest, extending to Australasia and the USA. *Saissetia oleae* was described originally from olive trees, but it attacks other trees including citrus. Several species of *Metaphycus* (Encyrtidae) parasitize it, including *M. helvolus* (Section **8.2.2.5(p)**) and *M. bartletti* and also the aphelinine wasp *Coccophagus bartletti* (Walter, 1988a). *Microterys flavus* is a cosmopolitan parasitoid of several soft scales. Species of *Lecanium*, the terrapin scales, are often greenhouse pests, but *Parthenolecanium corni* infests the branches and trunks of orchard and parkland trees (particularly *Fraxinus* spp.) in Eastern Europe. Here a complex of >30 chalcidoid species parasitize it. *Pulvinaria innumerabilis* is the cottony maple scale, in which the eggs are deposited in a large, protruding, waxy mass. *Ericerus pela* is the Chinese wax scale, in which secretions from the males were used to make candles (Section **8.3.3**).

4.4 Biting Pests of Soft and Cereal Stems

Although a few specialized beetles are included here, the bulk of these pests belong to the Symphyta, and more abundantly to the Lepidoptera Pyralidae and the acalypterate Diptera.

4.4.1.1(a) COLEOPTERA; Scarabaeidae. *Euctheola rugiceps*. Sugar cane beetle. Some other stem-boring beetles. This species was formerly an important pest of cane in the southern USA and is noted here because of its unusual lifestyle. Adults bore into the base of the cane, just above the roots, where they lay eggs, and where the larvae feed. Their relatively large size ensures the death of the cane. *Euctheola* spp. attack maize and other cereals in North America (Borror *et al*., 1989).

Another beetle, *Dermolepida albohirtum*, destroys Australian sugar cane.

With the great increase in growing oilseed rape, two other beetle pests, the flea beetle, *Psylliodes chrysocephala,* and the boring weevil, *Ceutorhynchus pallidactylus*, have increased in numbers in Europe. They are afflicted by specialized ichneumons of the genus *Tersilochus* (Section **8.2.2.5(l)**; Barari *et al*., 2005). The stem-boring weevil, *Listronotus bonariensis,* is an important pest of rye grass pastures in Argentina, southern Australia and New Zealand.

4.4.1.1(b) HYMENOPTERA, SYMPHYTA; Cephidae. *Cephus cinctus*, *C. pigmaeus*. Wheat stem sawflies. Temperate pests of wheat. Firstly, there is the general point that sawflies, whether pests or otherwise, are confined mainly to temperate regions. This is odd, as most insect groups are more diverse in the tropics. *Cephus pigmaeus* is originally European, but is now also found in North America, particularly in the east. The life cycle is annual and similar in both species, but *C. cinctus* is the most important wheat pest from Alberta, Canada, to the Dakotas, USA (Nansen *et al*., 2005; Beres *et al*., 2011). It originally attacked various native grasses in western North America and adapted to Canadian wheat by 1895. It now affects winter and spring wheats as far west as Oregon, USA. Beres *et al.* (2011) give no comprehensive estimates, but annual losses of grain are probably about a million tonnes.

Most adults to emerge early are female and all-female broods have been found in Alberta, Canada

(Flanders, 1945). This influences their population dynamics considerably. They slit the young wheat stems just after these have elongated, placing eggs singly within the cavities of the upper two internodes. But they fail to discriminate attacked stems, so the progeny of several females may occupy a single stem. Larger females produce larger eggs. The mean AF is low, ~30 eggs/female in resistant, solid-stemmed wheats (Fortuna, Glenman and Lew varieties), but as much as 56 in non-resistant wheats (Marquis variety). But plants that ripen prematurely or late, as a result of extreme weather, cause larval death (Holmes, 1982). Larvae bore in the stem, consuming the parenchyma (Fig. 4.7) and causing dead heart in young plants, but more importantly loss of grain and premature ripening in older ones. Mature fifth instar larvae spin a hibernaculum at the base of the stem, often below ground level, spend the winter in diapause and pupate in spring. But they cannot reach the base in solid-stemmed cultivars, and at the latitude of Montana or farther north may fail to survive low winter temperatures (Morrill *et al*., 1994). Ploughing in the stubble, either in autumn or in spring, also kills them. However, the use of the low-disturbance Noble plough to reduce soil erosion facilitates their overwintering. Sometimes the edges of a field are uncut or unploughed, which although provides a reservoir population to initiate a subsequent attack, also conserves their parasitoids. Indeed, attack is usually greatest along field margins, falling away towards their centres (Nansen *et al*., 2005). Diversionary food plants, such as brome grass, have been grown at the edges of wheat fields as a successful trap crop (Section **13.2.4.7**) and here parasitoids of these sawflies reach high levels, so that they provide a semi-natural reservoir for biological control when left in place. But sawflies often survive within the field, so that as with wheat midges there may be a build-up of the pest.

Fig. 4.7. Larvae of the sawfly *Cephus cinctus* (Cephidae), an important boring pest of wheat in Canada.

Insecticides are ineffective, so Canadian populations of *Cephus* are currently reduced using the braconid wasp *Bracon cephi*. While the parasitoid's effectiveness is much influenced by weather (Holmes, 1982), it has great resistance to low temperature (Section **10.2.3.3**). The related *B. lissogaster* is frequent in Montana, USA. Both species are bivoltine, but second-generation wasps cannot reach their hosts if the latter are deep in the stems. Late ripening cultivars allow them to complete their second generation and hence build up numbers (Beres *et al*., 2011). They both survive winter above ground in the stems, but harvesting would normally destroy this refuge. A further parasitoid, *Eupelmella vesicularis* (Eupelmidae) attacks not only the sawfly but also *B. cephi,* and has been recorded from the Hessian fly, *Mayetiola destructor* (Section **4.4.1.1(f)**). The eurytomid wasp *Eurytoma atripes* has been reared from *C. cinctus, B. cephi* and *M. destructor* (Nelson, 1953). In *C. cinctus*, when parasitized and unparasitized larvae are found in the same stem, the former are more susceptible to cannibalism (Nansen *et al*., 2005). Competition for space in the stem results in but one surviving larva (Holmes, 1982). By contrast, in the pyralid borer *Scirpophaga,* first instar larvae avoid each other as they space themselves out on separate rice plants (Bandong and Litsinger, 2005). In the present case, however, the proportion of wheat stems in which there are several sawfly larvae also affects the dynamics of the parasitoids. In assessing levels of damage, the proportion of infected stems is the meaningful criterion. Growing oats or non-cereal break crops effects complete control, but naturally there are economic considerations. While these sawflies are poor migrants, they may still persist as reservoir populations in native grasses and thus attack wheat subsequently.

4.4.1.1(c) LEPIDOPTERA; Pyralidae. *Diatraea saccharalis*. Sugar cane borer. A New World pest of sugar cane and maize found from Argentina to Louisiana. Some other pyralid and noctuid borers. This and the next species are now often separated in the Crambidae, although other workers refer them to the Crambinae. Adult *Diatraea* have the odd habit of wrapping themselves in their own wings. The females, which have an ~25 mm wingspan, attach their eggs in masses of ~20–30 to the upper sections of cane. The larvae hatch in ~1 week and bore in; larger larvae also affect the lower sections. They complete their development in <1 month, pupating within the cane. In young canes, infestation causes reduced growth, dead heart symptoms and sprouting from axillary buds. Older canes may break in high winds. There are several generations per year, depending on conditions. In Mexico and adjacent parts of the USA, another pyralid borer, *Eoreuma* (= *Acigona*) *loftini*, causes damage to cane and also rice (Johnson, 1984). By the year 2000, this borer, which is highly resistant to insecticides, had spread though Texas to Louisiana in the USA. The braconid wasp, *Parallorhogas pyralophagas* has been imported from Mexico as part of a control programme, although its efficacy may be compromised somewhat in transgenic (GNA lectin) cane (Tomov *et al*., 2003).

Diatraea saccharalis is the major pest of cane in Louisiana, and although several resistant cane cultivars are available insecticidal application, usually with tebufenozide, is still necessary (Posey *et al*., 2006). Here, the selection of the appropriate cultivar, such as HoCP 85-845 and CP 70-321, can reduce the cost of insecticidal treatment considerably, and may be the only solution to infestation by *E. loftini*. *Diatraea saccharalis* is the only generally important cane pest in the Caribbean, where its numbers are normally reduced by *Apanteles* (= *Cotesia*) *flavipes* (Alam *et al*., 1971). This braconid wasp uses chemical stimuli from frass to locate its host. It was introduced from Asia into Barbados in 1967, where up to 15% of cane joints had been infested, reducing the cost of attack to about a third of the previous value. Even so, there are questions about the specific identity of this wasp (Walter, 2003). A further braconid wasp, *Agathis stigmatera*, and the egg parasitoid *Trichogramma minutum* attack the borer in the Gulf States. Another of its parasitoids the tachinid fly *Lixophaga diatraeae*, spread after *A. flavipes* was introduced (Rossi and Fowler, 2003). In the Gulf States, the fire ant *Solenopsis invicta* eats the juveniles. Because of the enormous weight of cane produced annually (often >50 tonnes/ha), and because of competition between cane plants, pests have less chance of causing crop failure, although loss of sugar can be significant. As in cereal crops, which are usually over-sown (Section **3.2.1.2(f)**), the death of one plant in a clump results in enhanced growth of the others, resulting in *yield compensation*. Typically, commercial varieties can withstand 30% loss of shoots before sugar production is much affected, but such a reduction rarely exceeds 10%. In factories, cane is crushed with huge rollers and the juice squeezed out, *Diatraea* and all. Since cane is propagated from cut sections these may spread the larvae, but simply soaking them in water for 72 hours gets rids of most of them. Several crops are normally taken from a single planting (Posey *et al*., 2006). In eating cane, *Diatraea* can be an irritating pest. It also attacks the stems of sorghum and maize so that small, domestic plots of these plants may become heavily infested near cane fields. There are several other stem-boring *Diatraea,* including *D. crambidoides, D. grandiosella* and *D. centrella*.

In India, crambine species such as *Chilo partellus, C. tumidicostalis, C. auricilius* and *C. indicus* damage more mature cane. *Chilo polychrysus* is generally distributed, affecting rice and maize, while *C. infuscatellus* is widespread and also bores maize and some grasses (Kisimoto, 1984). In India and South-East Asia, *C. suppressalis* mines rice, preferring thick-stemmed cultivars. In East Africa, there is a bewildering diversity of such stem-boring moths (Le Ru *et al*., 2006), who discovered 44 noctuid, 33 crambine, 31 pyraloid and 25 tortricid borers in grain crops and wild grasses, sedges and reeds. Another pyralid moth, *Maliarpha separatella*, is a widespread rice borer in sub-Saharan Africa. *Chilo partellus* invaded East Africa before 1930, and together with the native *C. orichalcociliellus*, which it is apparently displacing (Ofomata *et al*., 1999), bores maize and sorghum. *Busseola fusca*, which *C. partellus* is also displacing (Kfir, 1997), and several *Sesamia* spp. (Noctuidae), also can be serious pests (Kfir *et al*., 2002). *Coniesta ignefusalis* attacks pearl millet in the Sahel.

Although there is naturally much variation, it is safe to say that these lepidopteran borers destroy >25% of all African grain, despite the presence of many parasitoids. For example, in maize in coastal Kenya, Zhou *et al.* (2003) recorded 40 such species. *Cotesia sesamiae*, *Apanteles flavipes* and *Goniozus indicus* (Bethylidae) were frequent larval parasitoids, while *Dentichasmias busseolae* (Ichneumonidae) and *Pediobus furvus* (Eulophidae) commonly attacked the pupae. A successful parasitic strategy is for the wasp to enter the tunnel and oviposit directly into the borer. *Apanteles flavipes*, in particular, which was re-introduced to East Africa in 1993, now suppresses *C. partellus* in maize from Mozambique to

Ethiopia (Assefa *et al.*, 2008), and because of trans-specific parasitism (Section **10.2.3.9**), probably has an effect on interactions between borers. Using genetic markers, these authors estimated its rate of spread to be >200 km/yr. Predation by spiders can be significant in the dynamics of these borers, for example on *C. partellus* attacking maize in the Punjab region of India (Singh *et al.*, 1975).

4.4.1.1(d) LEPIDOPTERA; Pyralidae. *Ostrinia* (= *Pyrausta*) *nubilalis*. European corn borer. A pest of maize from the Mediterranean to the Black Sea and in east and central North America. This borer (Fig. 4.8) is indigenous to maize-growing areas of the Old World. Pioneering spatial studies by W.R. Thompson *et al.* from 1919–1928 show that different regions of Europe the moth is suffer diverse suites of mortality factors (Thompson and Parker, 1928a; Thompson, 1929). It reached the USA in ~1917 (Krebs, 1972), Quebec, Canada, in 1927, and by 1950 affected 36 US states. By 1980 it reached Alberta, Canada (Lee, 1988). It is now one of the most serious pests of maize east of the Rocky Mountains, causing annual losses >US$1 billion, rapidly evolving ecotypes adapted to various regional conditions, and resisting all attempts at biocontrol (Section **13.2.4.6**).

Fig. 4.8. Boring larvae of *Ostrinia nubilalis* (Pyralidae), which can be a devastating pest of maize, particularly in North America. The photograph shows a young larva boring into the stem. Reproduced with permission from Clemson University – USDA Cooperative Extension Slide Series.

Mating occurs within a few days of emergence, often in grassy areas adjacent the fields. Then, females deposit batches of up to 50 eggs on the lower surface of maize leaves, the mean being ~20 under experimental conditions (Malausa *et al.*, 2008). It rarely affects sorghum and sunflowers. Warm, dry conditions kill the eggs (Lee, 1988). Young larvae move between plants and feed on leaves before entering stems as third instars (Gould, 1998), perhaps assessing their suitability before further committing themselves. In Europe, Thompson (1929) found 85–95% of young larvae died and Lee (1988) found 55–90% in Alberta, Canada. But several larvae often survive to bore a single stalk. Mature fifth instars overwinter within the stems, seeking the bases where conditions are less cold, in fallen ears or in the stems of weeds big enough to contain them. In spring, they excavate a pupation chamber close to the plant's surface from which the adult can escape. There are up to five annual generations in warmer parts of their distribution, but only one in the most northern parts. Univoltine and bivoltine races exist at similar latitudes both in Europe and North America, the former having an obligate diapause as late larvae.

Corn borers are afflicted by many parasitoids, some being European imports, but they kill few larvae. *Trichogramma maidis* and *T. evanescens* may attack the eggs, but Lee (1988) did not find them in Alberta. *Chelonus annulipes* and *Macrocentris cingulum* (= *grandii*) (Braconidae) (Lee, 1988; Godfray, 1994) and *Exeristes roborator*, *Eulimneria crassifemur* and *Dioctes punctoria* (Ichneumonidae) affect the larvae. In Quebec, *Eumea caesar* parasitize larvae and *Labrorynchus* spp. the pupae (Hudon and LeRoux, 1961). *Lydella thompsoni*, *Exorista mitis*, *Zenillia roseanae* and *Nemorilla* spp. (Tachinidae) are found in Europe.

Although leaf feeding by the young larvae is trivial, older larvae cause arrested growth when they tunnel in the stem, and the cobs to fall when they bore into them. Any insecticidal spraying needs accurate timing so that the moths are hit during oviposition and the young larvae killed while feeding externally. Similar accuracy is required, for example, in the control of clover weevils (Section **6.2.1.2(a)**). As with several other pests of soft stems, these structures provide the overwintering site, leading to control measure of smashing them and/or ploughing them deeply into the soil. Traditional practice in parts of France and Italy is to use late season stems as litter, or to shred them for cattle food. Some maize cultivars, especially when young, have a high natural content of an antifeedant, the quinone DIMBOA, and show natural resistance. A high silica content, which is a common inclusion in grasses (Section **13.2.4.2**), also improves resistance. More than 100 cultivars showing some degree of resistance to this borer are available. Those expressing *Bt* toxin are particularly useful, although recently it has begun to compromise some of them (Alves *et al*., 2006). Even so, redistribution of the adults and their failure to find food may be the major factor in the dynamics of this moth (LeRoux *et al*., 1963; Lee, 1988).

In Europe, a sibling species of *O. nubilalis*, *O. scapulalis*, lays most of the eggs on hops, but also a few on maize (Malausa *et al*., 2008). The Asian borer *O. furnacalis*, which also attacks maize, some other cereals and ginger, is important in South-East Asia, Indonesia and south to eastern Australia. Mitochondrial DNA studies indicate two sympatric races. The pyralid stem borers *Scirpophaga* (= *Tryporyza*) *innotata* and *S. incertulas* are pests of rice from India to northern Australia. Its susceptibility to these occasional pests depends on cultivar and stage. In *S. incertulas,* young rice transplants are too small to support the boring larvae, but become vulnerable as they grow (Bandong and Litsinger, 2005). A further susceptible stage occurs as the panicles are exerted.

4.4.1.1(e) DIPTERA; NEMATOCERA; Cecidomyiidae.

Contarinia spp. Wheat stem midges. Temperate pests of cereals. Several *Contarinia* spp. attack cereals. Pests of these crops when they reach a height >30 cm were originally hard to spray except from the air. The latter is costly since the planes and the pilots, who daily risk their lives in them, are expensive. In the tropics, spray pilots rarely reach the age of 40 (D. Lindo, personal communication, 1992, who did!). But in recent years sprayers with tall thin wheels that do little damage to crops, and a long folding boom are in general use. A further method, largely historical now, was to burn insecticidal candles, blanketing the field with smoke. On evenings with little wind this worked well against small dipterans. Midges are very short lived, however, so that the bulk of the population is in an invulnerable pupal stage in the soil, a situation common to all *Contarinia*. Since wheat is often grown continuously in the same field, pupal populations of this midge may build-up, making crop rotation an effective control. Another midge, *Orseolia oryzae*, attacks the basal stem of rice, although crop rotation in paddies is not usually practised (but see Section **13.3.2.2**).

4.4.1.1(f) DIPTERA; NEMATOCERA; Cecidomyiidae.

Mayetiola (= *Phytophaga*) *destructor.* Hessian fly. A major, cosmopolitan pest of wheat. Worldwide this is a most destructive pest of wheat, although some cultivars are resistant. Females lay up to 500 eggs in small batches on young wheat leaves, three to five being normal when food is abundant. Often, >95% of the egg load is laid. The larvae feed on the stems from behind the leaf bases: hence being classified here as internal feeders. Stimulants for oviposition are 1-octacosanol and 6-methoxy-2-benzoxazolinone (MBOA). But windy conditions interfere with oviposition by these frail flies and oviposition is deterred on plants already attacked. Egg and larval mortality are high and density dependent in culture, approaching 80% in large batches (Withers *et al*., 1997). This probably occurs in the field only when egg laying sites are short. Even so, the resultant stunting gives a greatly reduced yield of grain. Hessian flies are true gall formers as they induce the growth of a specialized nutritive tissue functioning as a metabolic sink for photo-assimilates (Harris *et al*., 2006). Their attack on actively growing leaves may well be essential for such development.

A second or even a third generation of the midge affects early sown winter wheat, so that later sowing dates avoid infestation. But unlike *Contarinia,* puparia remain on the plant beneath the leaf sheath and may pass the winter in this way, leading to a different control concept. Infected straw must be destroyed to prevent the springtime emergence of these flies and should never be transported. This imperative was broken inadvertently in 1776 when Hessian mercenaries, involved in hostilities in America, brought straw and *Mayetiola* pupae with them. Two years later the midge began to destroy wheat fields. But these insects, like most midges, have a short adult life so that if wheat is planted after their emergence the pest becomes innocuous (Wilde, 1981). Resistant wheat varieties are effective against it since while females oviposit on them the larvae fail to feed (Morill, 1982, in Larsson and Ekbom, 1995). Resistance genes, such as H5, H6, H9 and H13, may each be deployed successfully for a period of 6–8 years, after which they should be changed (Foster *et al*., 1991).

The larvae of a few, small, acalypterate dipterans bore the stems of temperate grasses and cereals. Apart from those dealt with below, several minor pests in *Oscinella*, *Geomyza*, *Meromyza* and *Cetema* also alternate between grasses and cereals (Jepson and Heard, 1959; Southwood and Jepson, 1962). See this early paper to appreciate the complexity of the fly fauna of grasses and Section **4.4.1.1**(**c**) for that of the pyralid borers of tropical Gramineae.

4.4.1.1(g) DIPTERA; CYCLORRHAPHA; **Chloropidae.** *Oscinella frit.* Frit flies. Normally a temperate pest of cereals and pasture. These small black flies are significant pests of wheat, barley and oats, the major temperate cereal crops. Densities may reach 2 million/ha in winter wheat, 8 million/ha in grass ley and 20 million/ha in the panicle stage of oats. There are also reservoir populations on various grasses. Frit flies are important on oats in the UK, on barley in Germany and on wheat in Russia (Jepson and Heard, 1959). Maize, a cereal of continental warm-temperate, Mediterranean and even tropical climates, is also attacked. In pasture, their effect is often to reduce the vigour of preferred grasses, allowing the ingress of weed species (Henderson and Clements, 1979). As expected, some grasses and their cultivars are resistant to attack by reason of the amount and distribution of the siliceous granules (Section **2.4.2**) they contain.

In autumn, these flies oviposit in a wide variety of situations: on stubble, weedy grasses such as *Holcus molis, Agrostis* spp., *Festuca* spp., *Poa* spp. and *Agropyron* spp. and on *Lolium* spp. and *Poa annua* in leys. The larvae also overwinter in winter wheat. They are often attacked by the peculiar, apterous braconid wasp, *Chasmodon apterus*, but also by facultatively predacious nematodes such as *Panagrolaimus rigidus* (Moore and Hunt, 1987). Such nematodes may be more frequent in grazed sward, as they are also found in the faeces of livestock. Even so, crops are likely to be attacked heavily after ley rather than under hay (Jepson and Heard, 1959). Flies emerge in April and May, and if the weather is mild they oviposit directly on cereal plants, or the fertilized females immigrate from grassy areas. The young larvae bore into the centre of the stem causing death of the tiller, which turns a conspicuous yellow, a condition called ‘dead heart symptom’. Survival depends on the age of the young plant attacked (van Emden and Williams, 1974). Second-generation flies emerge in May and early June and may oviposit on spring-sown cereals. Naturally, the length of the life cycle depends on latitude and annual variation in the physical environment. Second- and third-generation flies oviposit on oat panicles and the larvae feed on the developing grains, giving a final generation in late August and early September.

Damage is often greatest to late spring-sown cereals, not to winter cereals. Temperature differentials between the soil and the air affect the plant and the fly larvae differently, as in beet leaf miner (Section **5.2.2.2**(**a**)). Warm air and cold soil favour insect attack but limit plant growth. Severe damage often follows when wheat is sown after ley, as the larvae migrate through the soil after the grasses have been ploughed up. In the UK, it has long been known that sowing times can greatly influence the ensuing level of attack: (i) if winter cereals are sown in October they are unavailable to third or fourth generation flies; and (ii) for spring-sown cereals, the sowing date affects the percentage of plants attacked. In southern England, UK, the following results were obtained: before 15th March <5%, 23rd March ~10%, 31st March ~20%, 14th April ~32% (Jones and Jones, 1984). But in southern England, currently very few spring wheats are sown.

Movement through the soil is a peculiar feature of this pest (Jepson and Heard, 1959). Larval densities in rye grass ley have been estimated at ~250/m^2, which were followed after ploughing by a density of only 28/m^2 in winter wheat. Since this was after reproduction, only ~10% of the larvae had transferred successfully. Larvae seeking food are also vulnerable when sprayed, and those in stems are attacked by at least six species of parasitic wasps. During warm weather countless millions of these little flies migrate high in the air (Johnson *et al*., 1962). Other congeneric species are *Oscinella pusilla*, *O. germinationis*, *O. vastator* and *O. albiseta*, which tend to be specific to particular species of grasses. *Meromyza saltatrix* occurs in France in early sown winter wheat, while *M. variegata* often bores the common grass *Dactylis glomerata*.

4.4.1.1(h) DIPTERA; CYCLORRHAPHA; **Chloropidae.** *Chlorops pumilionis* (= *taeniopus*). Gout flies. A European pest of cereals. This fly attacks a broad spectrum of graminaceous plants, including wheat and barley. The adults have a yellow thorax with three dark brown vittae, making them easy to spot, although several other chloropid flies are patterned similarly. There are two annual generations. Eggs are laid on leaves in May/June and the young larvae bore into the stems of spring wheat causing a swelling (hence gout fly) and dead heart. The stems often fail to extend, the ear is small and may remain trapped within the flag leaf. Second-generation flies lay eggs on grasses, early sown barley and winter wheat in September. Gout flies overwinter as larvae, pupate in March/April and emerge in late spring, according to prevailing temperatures. There is a considerable shifting of its populations between various graminaceous plants. Late sowing in October avoids infestation of winter wheat, while if spring cereals are sown this should be as early as practical. Two hymenopteran parasitoids, *Stenomalina micans* and *Coelinus niger* attack the larvae, but at levels insufficient to effect control.

Another fly, formerly a stem borer of various wild grasses, *Opomyza florum*, has become more serious since the planting of more winter wheat, since it oviposits therein in late summer. This shows that changes in agricultural practice can generate new pests. Sampling adults in June from 1971–1979, Vickerman (1982b) found high densities in winter wheat, and as with gout flies, especially in those fields planted in early October. While in four outbreak years some fields had peak numbers exceeding 100/m^2, mean numbers over a total of 281 fields were <34/m^2 and in most years they were much lower, falling sharply in August. There were relatively few in other cereals and grasslands. *Opomyza florum* affects winter cereals in other parts of Europe (Pavlyuchuk, 1969), and evidence suggests that it spends much of the summer in wooded areas, before migrating to winter wheat in late September. This could explain its decline in fields.

4.4.1.1(i) DIPTERA; CYCLORRHAPHA; Muscidae. *Leptohylemyia coarctata*. Wheat bulb fly. A European pest of wheat. This is a larger insect, although rather small for a muscid fly, but familiarly grey and bristly. Adults fly in June and July and lay about 50 eggs on bare soil. Peculiarly, these eggs diapause until February, suggesting that they have an exceptional ability to resist desiccation. The young larvae wander through the soil to find the base of the wheat plant. As in cabbage root flies, to which this beast is related, attraction is by root exudates. Successful larvae feed in the central shoot causing it to swell. If winter wheat is sown in October, the plants are normally sufficiently well established, with two to four tillers in February, to resist attack. But if it has to be sown late then it is desirable to use dressed seed if there is a reasonable expectation of attack.

4.5 Sucking Pests of Soft and Cereal Stems

The majority of pests in this category, as in Section **4.3**, are Hemiptera. Those that also attack apical leaves will be considered in the next chapter (Section **5.3**). The membracid bug, *Stictocephala bubalus* (Section **4.3.1.1**(**a**)), which attacks fruit trees, completes its development on soft stems, and *Icerya purchasi* (**4.3.1.1**(**e**)) is occasionally found on the soft stems of various plants, including sugar cane.

5 The Pests of Leaves

5.1 General Introduction

As we saw in Chapter 2, gymnosperms contain relatively few species but form an extensive biome in the Northern Hemisphere, otherwise angiosperms are generally dominant. Their leaves emerging from germinating seeds are termed cotyledons (Section **2.3.2.3**). They are paired in dicotyledons, the majority of families, and single in monocotyledons (grasses and sedges, palms, bananas, orchids, etc.). They often contain metabolic reserves for the young plant, which are quickly expended or translocated to the roots. In many monocotyledons, however, metabolic stores are retained in a separate embryonic tissue, the endosperm. While cotyledons are normally the primary sites of photosynthetic production, this function is quickly taken over by the developing leaves. Stems can be photosynthetic too, and protein synthesis takes place wherever growth occurs. The leaf can be thought of as a unique heat engine (Spanner, 1963), its chloroplasts using solar energy for synthetic work. Pests attacking this engine reduces its efficiency according to leaf area destroyed and age. When cotyledons, buds and young leaves are damaged, their future production is denied to the plant. But compensation in the form of new leaves occurs as long as the plant has adequate water and nutrients (Herms and Mattson, 1992). Only after a leaf is about half developed does it begin to export its products to the rest of the plant. Although leaves are present for an extended period during the growing season and in evergreens and conifers last 2 to 3 years or more, their quality as food varies considerably, often being greatest just as they reach full expansion. Insects feeding on leaves fall into two broad categories (White, 1976): (i) those attacking young, nearly mature leaves (so tending to be apical); and (ii) a smaller group specializing on old senescent ones (so tending to be distal).

Leaf pests comprise a big section of *biters*, either *munchers* or *miners*, and a small section of *suckers* that are mainly apical and use their sophisticated mouthparts to tap into the plant's vascular system. While the latter are less diverse, and predominately homopteroid, they include many species whose chief importance is that they transmit pathogens such as plant viruses and phytoplasmas (Sections **1.6** and **5.3**). Although several biting pests also transmit pathogens (Ossiannilsson, 1966; Fulton *et al*., 1987; Nault, 1997), sucking ones do so more frequently. This is because homopteroids, having become infected earlier, inject saliva along with these pathogens into another plant when feeding again (Weintraub and Beanland, 2006). Many such bugs neutralize the phenolic defences of plants by injecting polyphenoloxidase enzymes. Surprisingly, cellulose digestion in folivores is rare (Martin, 1991).

5.2 Biting Pests

5.2.1 Munchers

These insects chew the leaf from the outside. Evidence of *continuous feeding* along the leaf margin is known in fossils from the Upper Carboniferous, but *discontinuous feeding*, either marginal as perforations, did not start until the Cretaceous, presumably avoiding rapidly induced defensive compounds (Scott *et al*., 1992; Section **2.4.2**). Non-marginal feeding requires more specialized mouthparts. Today the large majority of herbivores feed on seed plants, and the few that feed on ferns often belong to ancient orders (Cooper-Driver, 1978). Leaf munchers are somewhat unusual among pests as they are exposed on the surface of the plant (exophytic), and are variously coloured and patterned. They are often cryptic and hence normally green and/or brown, which blends in with the plant. More rarely they are aposematic (q.v.) and in general distasteful to vertebrate predators (Sections **5.2.1.3(b)** and **10.2.3.5**). Even so, they are on average much larger, and suffer 5–10% greater juvenile mortality, particularly from enemies, than concealed pests do (Cornell and Hawkins, 1995). Most pests of other plant organs are hidden, either because they bore into them (endophytic) or attack them beneath the soil. Endophytic pests are usually depigmented, yellowish or brown. One regards external pests of leaves as normal only because they are visible and familiar. Although most munchers prefer younger leaves and a minority older ones, if their food becomes short all leaves and even part of the stems may be consumed if the munchers are large.

On sub-dividing these pests by taxon, we find that many of *the biting exopterygotes are polyphagous or generalized*, attacking a wide variety of plant species and apparently being able to overcome all their standing and induced defences (Section **2.4.2**). Their juveniles are *nymphs*, and as usual often feed in a similar place and manner to the adults. Locusts are the most important group. *Endopterygotes*, on the other hand, in which the damaging organisms are mainly but not always *larvae*, show varying degrees of feeding specialization: from monophagy to polyphagy (Section **2.4.1**). While a majority of Neotropical caterpillars are specialists, those of many temperate Noctuidae are highly polyphagous. Thus, were we to divide endopterygote munchers into generalized and specialized feeders, as we did with root pests, it would produce an unhelpful classification. As an initial split we deal with them by major taxon.

5.2.1.1 Exopterygota: Generalist feeders

5.2.1.1(a) ORTHOPTERA; Acrididae. *Schistocerca*, *Locusta*, *Nomadacris*, *Melanoplus*, *Austroicetes*, and other genera. Locusts and plague grasshoppers. Tropical, sub-tropical or warm-temperate pests associated with deserts and grasslands. Although locusts are considered in some detail here, students should appreciate that tens of thousands of pages of research about them have been amassed. While we know so much, they remain formidable. In total this family comprises ~10,000 species. The Orthoptera date from the Upper Carboniferous and were probably the first leaf feeders (Scott *et al*., 1992). Grasshoppers and locusts have evolved as major herbivores in grassland and desert biomes (Uvarov, 1977). In contrast to the related family Tettigoniidae, which feed at night and are seldom pests (Price, P.W., 1997), they are mainly diurnal, polyphagous herbivores, frequently forming outbreaking populations. Roughly speaking, locusts are big grasshoppers that are sometimes capable of mass migration and as adults are almost unrestrictedly polyphagous. Specifically speaking, plague grasshoppers such as *Austroicetes* and *Melanoplus* have diapausing eggs; true locusts such as *Schistocerca*, *Locusta*, *Nomadacris* and *Chortoicetes* do not (Andrewartha and Birch, 1954). Even so, the eggs of true locusts may remain quiescent in dry soil for some time, requiring only to absorb water before they hatch. Eruptive populations of these insects exploit grasslands, growing quickly after rains and on reaching plague densities migrate hundreds, sometimes thousands, of kilometres into other biomes, often suffering great attrition.

Locusts breed in the world's great deserts and their Sahel, grassland or savannah margins where they try to track sporadic rainfall (Section **2.2.3**). *Outbreak areas*, where swarms form, are rather well-defined localities often favourable to reproduction, but their extent varies greatly according to rainfall and hence so does their ability to generate massive swarms. These localities are surrounded by *invasion areas* into which swarms migrate (White, 1976). *Recession areas* are regions in which migrant locust dwindle in numbers, normally due to continuing drought or excessive moisture. They are *sink habitats* (Section **9.4**). Several species tend to outbreak synchronously, compounding the destruction they cause (Showler, 1995). In Africa, plagues may reach far from the Sahara to the Eastern Highlands and the Congo Basin where rainfall is high. Afro-Asian species are the best studied, as a result of political, as well as agricultural, pressures during the twentieth century, but in Australia several species continue to be intensely researched. By contrast, the South American species are poorly known. During winter or the dry season (or both), most populations exist as long-lived adults in true locusts but as diapausing eggs in plague grasshoppers. During egg laying the ovipositor operates as a semi-autonomous digging machine (Thompson, 1986), boring deeply into the soil and pulling the abdomen out to its limit of ~10 cm, an activity that may take >1 hour. The intersegmental membranes allow stretching of up to tenfold. The eggs are buried *en masse* and covered with a viscous secretion that hardens to form a protective egg pod. In China, early stage eggs of *Locusta* have surprising resistance to low temperature, their undercooling point (Section **10.2.3.3**) being lower than –20°C (Jing and Kang, 2003). When eggs were exposed to –10°C, the LD_{50} for the northern population (Liaoning, 41°N) was >160 hours but only 4 hours for the southern one (Hainan, 19°N).

In plague grasshopper eggs, wetting induces hatching when special hydropyle cells absorb water. There is a complex 'living valve' that allows active absorption but prevents loss (Andrewartha and Birch, 1954). The depth of burial relates to the amount of rainfall needed to reach the eggs, an amount that brings forth a crop of grasses and therophytes (q.v.) upon which the young nymphs feed. Later on, when these plants become stressed by drought, it raises their amino-acid levels, and hence provides better food (White, 1976). But when amino-acid levels are low, a high percentage of the young nymphs die.

Species of *Scelio* and *Sinoditella* (Scelionidae) (Section **8.2.2.5(w)**) parasitize the egg pods. In Australia, *Sc. chortoicetes* attacks *Austroicetes cruciata* and *Sc. fulgens Chortoicetes terminifera*. *Scelio* spp. also afflict *Melanoplus* spp. in North America. In western Canada, *Blaesoxipha atlanis* (Sarcophagidae) often parasitizes *M. sanguinipes*, but both insects may survive the encounter (Danyk *et al*., 2005a). *Stomorhina lunata* (Calliphoridae), following the swarms, parasitizes the egg pods of the desert and migratory locusts. Some species of *Scelio* travel at heights up to 300 m in air streams. In parts of Africa and Asia, the histerid beetle *Saprinus ornatus* may consume a high proportion of locust egg pods (Rainey, 1989). Although big asilid flies and dragonflies attack locusts (Stortenbecker, 1967, in White, 1976), they fail to restrain them. Birds and rodents often eat grasshoppers, while under humid conditions these insects are particularly vulnerable to fungal pathogens. Work continues on using the fungi *Metarhizium ansopliae*, *M. flavoviride* and *Beauveria bassiana* to control them (Showler, 1995) and they have been experimentally infected with the bacterium *Serratia marcescens*. However, desert locusts employ their gut microflora to counteract this fungus. But overall, the influence of enemies is minor compared to the massive effects of weather (Popov, 1965; White, 1976; Rhoades, 1985; Skaf *et al*., 1990), and consequent migratory losses.

Before the Russian Revolution in 1917, Boris Uvarov was engaged in grasshopper research in the extensive grasslands in the south of the country. He and V.I. Plotkinov were the first to recognize locust *phases*. Working on *Locusta migratoria* and the supposedly related *L. danica*, they found that eggs of the former often developed into adults of the latter, and that young *danica* nymphs grown in crowded conditions could develop into *migratoria*. There is only one true species, so *danica* was renamed the *solitaria* or short-winged, non-migratory phase and *gregaria* the long-winged, migratory phase of *L. migratoria*.

Phase difference in locusts has been regarded as an example of alary polymorphism, which occurs in many adult insects (Harrison, 1980; Roff 1986, 1994; Section **1.4.3**), such as numerous female aphids, water boatmen, crickets, carabid beetles and parasitic wasps. Morphs may either be winged or wingless. However, locust phases are not so extreme and do not obey Ford's definition of polymorphism (Section **1.3.3**). Measurements of forewing length, head width and femoral length overlap widely (Kennedy, 1961a). Therefore, the term '*phase*' and not '*morph*' is better, although sometimes the ambiguous term '*phase polymorphism*' occurs. Maeno and Tanaka (2008) and Pener and Simpson (2009) following Pener (1991) discuss the subject in detail, adopting the better general term *polyphenism*. Note also that the *solitaria* phase of *L. migratoria* can still fly well but, like that of *S. gregaria* (Ibrahim, 2001), does so at night and normally it is only its *gregaria* phase that forms huge cohesive, diurnal swarms.

In all insects showing alary, or better, *flight polymorphism*, the migratory morph is specialized to search and find new habitats. Their juvenile stages are generally darker and grow more rapidly, as in the larvae of *Zeiraphera diniana* and *Spodoptera exempta* (Sections **5.2.1.4(d)** and **5.2.1.4(i)**). Despite this, in locusts there are *discontinuous* colour and behavioural differences between the phases that become obvious in the nymphs. With respect to these characters, there is true polymorphism. Also, while achieved fecundity (AF) is greater in *solitaria*, the hatchlings are heavier in *gregaria*. The detailed work on the factors determining these phase changes in locusts was undertaken with a view to preventing the development of their devastating migrations.

Along with several other street-wise Russian biologists, the great geneticist Dobzhansky being another, Uvarov fled to the Western democracies about the time of the Revolution, so avoiding the subsequent inquisitorial ravages of Stalin and his henchman Trofim Lysenko. Times had been hard. Although employed as a biologist, at one point Uvarov (later Sir Boris) was reduced to selling home-made pies in a Tbilisi market in order to make ends meet! He brought with him the talented Waloff sisters (Nadia and Zena) and was instrumental in setting up the

Anti-Locust Bureau in London in 1929 in response to pleas from East African farmers for help in combating plagues. The Bureau became the Anti-Locust Research Centre in 1945, and later the Centre for Overseas Pest Research. Lately, work continues under the Food and Agriculture Organization of the United Nations (FAO). Some of their work is given below for the three main African species, *S. gregaria*, *L. migratoria* and *N. septemfasciata* (Anon., 1982). Locust plagues are usually simply defined by the number of countries affected. They may last for 15 years and in *S. gregaria* continued for much of the twentieth century and into the twenty-first century. At their peak, swarms have been reported from ~40 countries in a single year, but during recession only from two or three. Apart from the authors referenced here, extensive work on these locusts has been done by J.R. Riley and H.J. Sayer in Africa, and by Y.R. Rao and M.V. Venkatesh in India. See also Chapman and Joern (1990).

5.2.1.1(b) ORTHOPTERA; Acrididae. *Schistocerca gregaria gregaria* (= *peregrina*) and *S. g. flaviventris*. Desert locusts. This large locust, with females 50–60 mm long, multiplies in the vastness of the Sahara (Showler, 1995) and other arid regions through Saudi Arabia to India (Section **2.2.3**). The area of the Sahara and the adjacent Syrian and Arabian deserts is approximately 12 million km^2 and hence far greater than that of Australia (7.7 km^2). Betts (1976) gives detailed maps of the distribution of 'hopper bands', and hence outbreak areas, based on 25 years data and covering an area >20 million km^2. These must be one of the most extensive spatio-temporal data sets ever presented for an insect. Recently, there have been plagues from 1986–1989, 1992–1994, 1996–1998 and 2003–2004 (Ceccato *et al*., 2007; Pener and Simpson, 2009). Although swarms arise anew from *solitaria* phase populations (Ibrahim, 2001), outbreak areas are less permanent than in the migratory and red locusts. Desert locust migrants seek a shifting, unpredictable food resource where rain has just fallen (Skaf *et al*., 1990; Pedgley *et al*., 1995), but tend to be more northward in the northern summer. They affect the Atlas region and scattered sites in Asia Minor through to the Thar Desert, with a limit of about 20–35°N. But a major outbreak area persists in the Horn of Africa. Then in late summer, breeding becomes concentrated at the Inter-Tropical Convergence Zone (ITCZ; Section **2.2.2.1**) along the southern Sahara centring at 17°N, but especially in parts of Ethiopia and the southern Sudan, while the Thar Desert becomes another hot spot. In December, breeding generally becomes confined to Somalia and the banks of the Red Sea. But a population breeding on the Niger floodplain in May–July often migrates ~1000 km north into the Sahara and breeds there from January–March. Spring breeding associated with Mediterranean rains occurs in Morocco, Algeria and in Asia Minor (Farrow, 1990, and Magor, 1995, in Drake and Gatehouse, 1995). Surely, research will reveal further complications.

Other migrations, mostly driven by seasonal winds, link the outbreak areas. Apart from Köppen's (1873) idea that locust plagues are associated with the 11-year sunspot cycles, plagues are usually regarded as having unpredictable frequency, but Cheke and Holt (1993), using spectral analysis, suggest a 16-year cycle. Ibrahim's (2001) model of this boom-and-bust system suggests recessions of 10 ± 3 generations with swarming periods about half this duration, but these are more variable. Look at the map: the Sahara alone is ~5000 km from east to west and ~3000 km from north to south. It is about twice as big as Australia! Historically, the Red Sea region has been a frequent source of plagues, '… strong west wind, which took away the locusts, and cast them into the Red Sea …' (10 Exodus: 19). While in the Qur-ān, verse 7–133, Surat l – raf, they are recorded as plagues on the Egyptians, '… we sent upon them the flood and locusts … but they were an arrogant and criminal people'. Then Augustine in his *City of God* about 427 AD records a huge and formidable swarm, having eaten everything, drowning in the sea. Records exist of their dead bodies being washed ashore in mounds up to 1.5 m high, producing an appalling stench. Ugandans, however, celebrate such events: one, more appropriate name for Lake Victoria, is 'Rwitengenze', Killer of Locusts.

Desert soils rich in clay have the greatest retention of water and often support coarse perennial grasses and other plants suitable for adult food and shelter. The young hoppers, however, require a more tender diet, befitting their smaller size and weaker mandibles. Those grasses and therophytes that grow on sandy soils after rain provide this diet. Desert locusts require such soils for oviposition, but data are particularly clear for *Dociostaurus maroccanus*, the Moroccan locust (Uvarov, 1977). As above, when these plants dry up they become amino-acid rich and so better quality food (White, 1976). In *solitaria*, the egg pods contain 70–100 eggs and a female may deposit four to five pods, a high fecundity for an insect. Such females lay more but slightly smaller eggs the larger their size, whereas larger *gregaria* females lay more *and* larger eggs (Maeno and Tanaka, 2008). But in the field, as in several locusts, the proximity of the two edaphic and hence vegetational types, namely environmental heterogeneity, improves the survival of the nymphs *and* increases AF. Hatching takes ~2 weeks. The first nymphal instar is vermiform, allowing ascent through the sand, but at the surface it moults into a typical hopper. *Solitaria* nymphs are greenish (this phase was called *S. flaviventris*) while those of *gregaria* are strongly patterned black and orange. Naturally, stage duration is variable, but hoppers take ~5 weeks to mature. Their orientation behaviour adjusts the amount of insolation they receive and in turn their body temperature (T_b). In early morning they bask in the sun, exposing the maximum body surface, but later retreat into the shade of any plants or sit to present the minimum area to the sun (Waloff, 1963; Section **1.2**). At night they often aggregate in masses, a co-operative behaviour conserving heat.

Young adults, however, need several weeks to mature, during which they lay down a considerable fat body. In all, *solitaria* phase takes ~20 weeks per generation and *gregaria* phase ~18 weeks (Cheke and Holt, 1993). Migration of distinguishable 'young swarms' is common, but reproducing swarms also migrate. Maturation of the gonads is accelerated by the presence of certain terpenoids, particularly the more volatile monoterpenes, in the air (Hassanali *et al.*, 2005). These are produced prior to rain by the buds of shrubs such as *Commiphora* (myrrh) and *Boswellia* (frankincense). Egg laying commonly continues for a month or more. In *Schistocerca* and *Locusta*, males frequently remain *in copula* during oviposition, thus protecting their genetic investment. The *solitaria* females are particularly attracted to areas near *Heliotropium* spp. (Boraginaceae) and *Pennisetum* (Gramineae), while *gregaria* prefer open, moist sandy areas (Hassanali *et al.*, 2005). While several generations may be needed to build-up densities high enough to initiate the migratory phase, in *S. gregaria* such an increase can occur within a year. The *gregaria* phase has up to three generations/year and a strong tendency towards synchronous development, producing plague swarms that are more frequent and last longer than those of the other African locusts (Fig. 5.1).

Being such active fliers, migrating locusts need a great deal of energy, (Wigglesworth, 1984). Initially they use up a glycogen store, but then mobilize lipids from their fat body

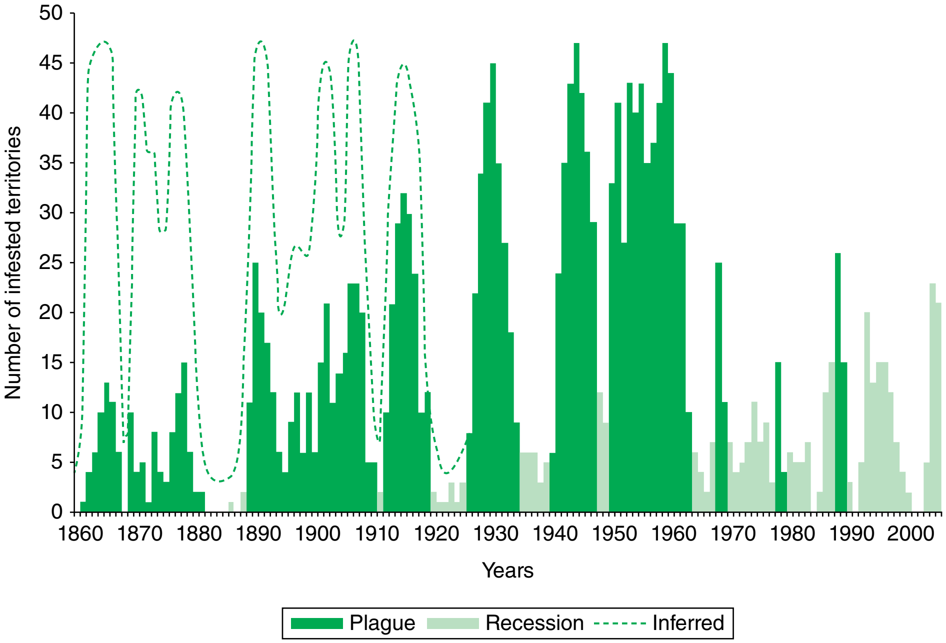

Fig. 5.1. Periodicity of the swarms of *gregaria* phase desert locusts, *Schistocerca gregaria*. From Cheke, R.S. and Holt, J. (1993) *Ecological Entomology* 18, 109–115; reproduced with permission.

(Goldsworthy and Joyce, 2001), that constitutes up to 10% of total body mass. In *Locusta*, and probably in *S. gregaria*, there are differences in the flight fuel metabolism in *solitaria* and *gregaria* (Ayali *et al.*, 1996), the higher lipid levels in the latter phase permitting iterative, migratory flight. But plant material is low in calories (Sections **2.4.2** and **10.2.2.5**) so a great weight is required daily to sustain them, even as great as that of the swarm. A large swarm contains many billions of individuals, weighs tens of thousands of tonnes, and has a biomass density of ~100 tonnes/km^2. Since an individual can live several months, one can see why the swarms are so destructive. Wigglesworth calculated that a little 15,000 tonne swarm would use as much energy per day as 1.5 million men would, approximately seven times the human rate of consumption. Locust swarms literally darken the sky: ‘the east wind brought the locusts ... they covered the face of the whole earth, so that the land was darkened; and they did eat every herb of the land, and all the fruit of the trees’ (10 Exodus: 13–15). But while the densities in flying swarms may reach 1 individual/m^3, they are normally in the region of 1/30–40m^3 (Rainey, 1989).

In sunshine, the ambient temperature range for flight is 15–40°C. Swarms often move at relatively low levels, with the leading edge of the swarm settling to feed or cool, being over flown by the remainder, and taking off again at the back of the pack (Waloff, 1972), and so on. Individuals have a sustained air speed of ~15 km/h. Double exposure photographs at 1/500 s apart taken beneath a swarm can be used to estimate their orientation and trajectory. A neural mechanism prevents mutual crashing. The swarms generally move within a few degrees of the wind direction, but because most individuals settle periodically or move to maintain a cohesive, migrating mass, their average ground speed does not exceed wind speed. In summer, breeding swarms often follow the ITCZ where rain is likely to fall (Rainey, 1951), providing an area rich in food. Convergent winds may make swarms coalesce. Betts (1976) recorded a swarm moving from an outbreak area in central Sudan in mid-September 1968, to Niger by early October and to Morocco by the end of the month, a distance >4000 km. They also migrate at heights of 1 km or more, in which case their flight path is governed entirely by the wind (Waloff, 1972). In mountainous areas they are recorded flying at 2.6 km above sea level. There are records of locusts being trapped by anabatic winds (q.v.) on the slopes of Mount Kilimanjaro at elevations ~2 km. While swarms usually track convergent winds that bring rain, occasionally fast winds associated with the ITCZ sweep them from the deserts altogether into invasion areas. These comprise broad bands to the north and south. In the north, Morocco (partly protected by the Atlas Mountains), Tunisia, Egypt, Jordan, Syria and Iraq are affected, and in the south, Guinea, Nigeria, Congo, Uganda and Tanzania. But they may go even further. In 1613 a plague fell in the Camargue and later moved north-west into the foothills of the Massif as far as Tarascon. Swarms from outbreak areas in the Arabian Desert and Pakistan reach fertile regions in Turkey, Iran and Afghanistan and east to Bangladesh (Ceccato *et al.*, 2007). In all, the invasion area embraces 29 million km^2 (Ibrahim, 2001). There are even a few cases of *Schistocerca* reaching the West Indies: I saw specimens in 1988 (see Rainey, 1989; Skaf *et al.*, 1990). In north-west India, local migration occurs during the monsoons and also involves *solitaria* phase locusts. An isolated population (= ‘*isolate*’) is found in the Kalahari Desert (*S. g. flaviventris*). It can have two generations during the October–April rains and swarms may penetrate South Africa.

Control measures must take account of the vast distances involved, that swarms ignore national boundaries, and of the difficulty for control staff to travel by land. Even today there are only three main roads that traverse the Sahara from north to south, while only one skirts its southern border from Dakar to Khartoum. Once it was known that outbreak areas generally occurred in wind convergence zones, planes equipped with Doppler radar wind-finding systems could ‘seek-and-strike’ them. For example, a DC-3, the old aerial war-horse, could fly 1000 km with 500 l of fenitrothion, enough insecticide to destroy a small swarm characteristic of up-surging populations. Their cohesiveness makes them vulnerable: a weak link, and their flight activity draws insecticidal droplets onto their bodies. On the ground, however, their closed wings give them some umbrella-like protection. But both hoppers and adults can be killed there with poisoned baits, although with large swarms thousands of tonnes are required.

Control tactics now centre with the FAO in Rome. The key points are knowledge, forecasting, organization and adequate finance (Ceccato *et al.*, 2007). Modifications to radar systems to improve tracking have been made repeatedly (Boiteau and Colpitts, 2004; Chapman *et al*., 2004). Prevention is far better than cure (Showler, 1995). Estimating swarm trajectories is key, and satellite imagery is used increasingly. But costs can be huge because of the scale of the problem: US$200 million for the 1986–1989 outbreak (Skaf *et al*., 1990). Because outbreaks are dependent on weather, long-range forecasts, which are now available, are fairly accurate in predicting them. But as Ceccato *et al*. (2007) point out, finance and infrastructure must be in place to achieve a rapid response. The spectral analysis of population numbers (Cheke and Holt, 1993) and modelling their boom-and-bust cycles (Ibrahim, 2001) are important steps that aim to facilitate long-range forecasts of an outbreak, allowing time to finance and organize controls.

Schistocerca americanum and *S. emarginata* (= *lineata*) occur in the southern USA and although sometimes migratory, they are seldom pests. Nymphs of the latter congregate on *Ptelea trifoliata* (Rutaceae) plants, obtaining defensive compounds from them and assuming yellow and black warning coloration. As in the desert locust, this is a density-dependent effect (Sword, 1999; Section **10.2.1**). *Schistocerca piceifrons* swarmed in Central America in 1986–1987 (Skaf *et al*., 1990), while *S. cancellata* (= *paranensis*) is found in the Argentinian pampas and adjacent countries. In 1946, a swarm in southern Brazil covered an area of 6000 km^2. In 1934, J.B. Daguerre was the first to show that swarms of this locust normally move *with the wind*, although this was not appreciated for other species until much later (Rainey, 1989). Such direction saves energy and increases searching efficiency (Dusenbery, 1989). *Schistocerca interrita* inhabits coastal areas of Peru, while *S. urichi* is found in Central America. All these species may have evolved long ago from immigrant populations of the desert locust. Another locust, *Rhammatocerus schistocercoides*, which had never been recorded to swarm, formed an outbreak in Mato Grosso in 1985 (Skaf *et al*., 1990). This may be related to the massive forest clearance that has occurred in that state.

5.2.1.1(c) ORTHOPTERA; Acrididae. *Locusta migratoria*. Migratory locusts. All the several sub-species of this locust seem to have outbreak areas in extensive grassland plains that are subject to alternate flooding and drought (White, 1976). Outbreaks are driven by occasional low mortality of the young nymphs, which otherwise is ~98%. *L. migratoria migratorioides* is slightly smaller than the desert locust, and found mainly south of the Sahara. Its major *outbreak areas are localized but variable in area*. They occur in the Upper Niger (Pedgley *et al*., 1995) just south of Timbuktu, along tributaries of the Upper White Nile and around the Awash River in Ethiopia. In the 1970s Lake Chad dried up, formed swamp grassland and became a new outbreak area, illustrating the ability of these locusts to search and find on a grand scale. Other such areas are scattered farther south, for example, in north Angola and south-east Zambia. The invasion areas embrace the North African coast and most of Africa south of the Sahara. Although this locust has usually only one annual generation, damaging swarms have formed. In 1955 a swarm 250 km long and 20 km wide arrived in Morocco, causing great long-term damage to citrus, despite the fact that grasses and sedges are its preferred foods; it has laid eggs as far north as Germany.

Locusta m. manilensis from China, the South-East Asian mainland and islands can have up to five annual generations (Jing and Kang, 2003). In China, it outbreaks in the Yangtze Delta in marshes associated with overflow channels. Historical data for the last millennium show that outbreaks occur after sequences of drought and flooding (Zhang *et al*., 2009). In the Philippines, its outbreak areas are interior grasslands, which are subject to periodically low rainfall. Then, *L. m. migratoria* from Central Asia is univoltine and diapauses as eggs during winter. An outbreaking population in Uzbekistan in the Amudaya River basin south of the Aral Sea, defined by Landsat imaging, feeds on the extensive reed beds of *Phragmites* (Sivanpillai and Latchininsky, 2008). Some 100,000 ha were infested in 2005, with gregarious phase nymphs reaching incredibly high densities of >1000 m^2. In Madagascar, *L. m. capito* has an annual, migratory cycle of about four generations. It tracks those regions made suitable for breeding by variation in rainfall, although gregarization occurs only in the southern tip (Lecoq, 1995). Parental effects may influence subsequent phases in that parental crowding induces earlier and larger offspring (Chapuis *et al*., 2010).

Locustana pardalina, the brown locust, found in southern and south-western Africa, also has solitary and migratory phases. Its outbreak area comprises ~250,000 km^2 of semi-arid pastoral country in the Karoo (Lea, 1969). As in the red locust (Section **5.2.1.1**(**c**)), a mosaic of short (*Cynodon dactylon*) and taller grasses (*Echinochloa pyramidalis*) and more elevated foliage is associated in such areas (White, 1976), which vary in relation to previous rainfall. Topography tends to drive this heterogeneity as it directs rainwater into low-lying areas (Section **10.1**). In the late 1980s this species invaded Botswana. The tree locust, *Anacridium melanorhodon*, inhabits a band across the southern Sahara from Senegal to Eritrea, and became a pest in Chad and parts of Sudan in the same period (Skaf *et al.*, 1990), often affecting fruit trees (Showler, 1995). *Dociostaurus maroccanus* often produces eruptive populations in west Turkey.

5.2.1.1(d) ORTHOPTERA; Acrididae. *Nomadacris septemfasciata*. The red locust. With the exception of the Upper Nile and Somalia, this large nomadic locust is found only in Africa south of the Equator, a region regarded as its invasion area (Gunn, 1960), although sea crossings to Mauritius and Reunion (and presumably Madagascar) have occurred. Swarms are not as massive as those of desert locusts, but can still be ruinous locally. Breeding areas are rather localized to the Rukwa rift valley in south-west Tanzania (Woodrow, 1965), where they multiply in grassy swamps (*mbuga*), the Mweru marshes of Zambia and the Chilwa plains of Malawi (Hill, 1983). Here, the prostrate *C. dactylon* provides ideal food and the associated clumps of *E. pyramidalis* nocturnal roosting sites. They also breed in parts of Zimbabwe and Mozambique. Much of the dry part of the year, March to October, is spent in adult diapause. Reproduction occurs in November and December during the rains. Maturing females gain considerable weight. Oviposition occurs mainly but not exclusively at night, and as in *Locusta* and *Schistocerca*, bare ground is selected. There are ~120 eggs/pod. These hatch in ~1 month and complete development in 2–3 months (Woodrow, 1965). High numbers are associated with low rainfall in the preceding year (White, 1976). This probably improves the nitrogenous content of their food. As in desert locusts, a mosaic habitat is ideal for swarm formation, here it is short and tall grasses. Localization of their outbreak areas and their relative accessibility, like *Locusta*, make them easier to control than desert locusts. Red locusts are attracted to grassy areas that have recently been burnt, a situation that can be used to entrap them. Also, swarms tend to become sedentary in areas of tall grass and sugarcane, because individuals lose mutual contact. Again as in *Locusta*, plagues have been sporadic. Other species of *Nomadacris* include *N. succinata*, the Bombay locust from India, and *N. guttulosa*, the spur-throated locust from Australia.

5.2.1.1(e) ORTHOPTERA; Acrididae. *Melanoplus sanguinipes*. Migratory grasshoppers and related species. In the north-western prairie states of the USA towards the end of the nineteenth century, this species became a scourge in a few isolated years, although it had a dramatic effect. The following are abridged excerpts from newspapers published in Kansas and Nebraska in 1874, taken from Evans (1970). They give graphic accounts of what it was like to be there on the ground when a swarm arrived.

> The noise of their coming resembled suppressed distant thunder or a train of railcars in motion and the noise of their chewing in the cornfield like that of a great herd of cattle. They even ate the bark of trees, weathered wood from the sides of barns, paper and dead animals.
>
> The insects came from the north west in unbelievable numbers. They were from four to six inches deep on the ground. Men were obliged to tie string around their pants to keep the pests from crawling up their legs. When they hit my face the impact was like a missile. They landed about four o'clock. By dark they had eaten 15 acres of corn and not a stalk was left. That night I slept in the barn. They ate my hat and the harness of the horses hanging up.

Small comfort that these swarms were probably modest in comparison to those of the desert locust, although one of them was estimated at 124 billion individuals. Since these spectacular outbreaks, however, such swarms have not re-occurred, but non-swarming populations still damage field crops.

Other American species of *Melanoplus*, which contains over 100 species, include *M. bivittatus*, *M. devastator*, *M. differentialis*, *M. spretus* and *M. femur-rubrum*, which occasionally cause crop damage. Despite the wide polyphagy of these and other grasshoppers (Waldbauer and Friedman, 1991), experiments (Caswell and Reed, 1975) on food quality in *M. bilituratus* using C3 and C4 plants (q.v.) showed the latter to be greatly inferior, AF dropping from ~170 to ~22 and survival being reduced in all instars. In Saskatchewan, Canada, *Camnula pellucida* nymphs invade and destroy marginal areas of wheat where these abut the prairie. *Dissosteira carolina*, the Carolina grasshopper, and *Brachystola magna*, the lubber grasshopper, represent further genera. North American species have annual life cycles, depositing eggs in late summer and feeding until killed by frost. They are susceptible to the microsporidian *Nosema locustae*, which has been used against them on rangeland in the western USA (van Emden and Service, 2004). Even so, this complex, which may comprise as many as 300 species in the western rangelands (Lockwood, 1993), is a generally beneficial part of a diverse ecosystem. It is only during occasional outbreaks that significant damage to grazing occurs. A suite of grasshoppers (*Orphulella speciosa*, *Syrbula admirabilis*, *Phoetaliotes nebrascensis*, *Melanoplus keeleri*, and several others) is important in the economy of tall grass prairie (Laws and Joern, 2012). Range management has significant effects on the species composition, density and parasitism of these species. Tachinid and nemestrinid parasitism varied with management and host species, the latter parasitoids producing a greater reduction in AF. *Coscineuta virens*, which has diapausing eggs, can be a pest in Trinidad.

5.2.1.1(f) ORTHOPTERA; Acrididae. *Austroicetes cruciata* and *Chortoicetes terminifera*. The Australian plague grasshopper and the Australian locust. The Great Australian Desert is driest in the middle (~100 mm mean annual precipitation [MAP]), and as one goes south towards the coast, MAP increases gradually. The south-west corner of the country is Mediterranean (~800 mm MAP). Of course, the rainfall varies from season to season, the *variation* usually being inversely related to MAP (Section **10.1.1**). Natural vegetation ends in the coastal belt, which was originally *Eucalyptus* forest and *Acacia*/*Atriplex* savannah, but much is now farmland. If the weather is too dry *Austroicetes* nymphs starve before maturity, but if it is too wet they suffer from fungal disease (Andrewartha and Birch, 1954). So in wet years this species tends to be more abundant in the north, but in dry years it moves south and plagues the coastal farmland. Indeed, during agricultural development the clearance of natural forest has produced a much greater area suitable for it than formerly.

Chortoicetes has several outbreak areas around the 32nd parallel to the North of the Grawler Ranges in South Australia, near Broken Hill, and in the headwaters of the Darling River on the New South Wales/Queensland border. It also breeds in the arid zone of Western Australia at ~20–25°S, after sporadic rains there have induced bursts of vegetation (Drake and Gatehouse, 1995). Daytime migrations are normally low level and downwind, covering tens of kilometres. Nocturnal migrations occur at several hundred metres altitude and cover a few hundred kilometres (Drake *et al*., 2001). As in desert and red locusts, a mixture of soil types and annual and perennial grasses results in high population densities. Tussocks of perennial *Stipa* and *Eragrostis*, which grow in clay soils, provide both shelter and food during drought. Satellite imaging has been used to identify such areas. Probably felling trees and planting exotic grasses for sheep ranging has materially improved the environment of this locust. Migrants are found commonly south of a line from Perth to Rockhampton in Queensland. In November 1989, *Chortoicetes* invaded the south-western crop lands, borne by strong north-easterly winds. In early 1990, the eggs hatched, after summer diapause, in plague proportions and despite spraying caused appreciable damage. A partial re-migration to the arid zone occurred later, but countless migrants were drowned at sea. *Phaulacridium vittatum*, *Gastrimargus musicus* and *Warramaba virgo*, a parthenogenetic species comprised entirely of females, are also Australian.

5.2.1.1(g) ORTHOPTERA; Acrididae. *Zonocerus variegatus*. The variegated grasshopper, a broad-spectrum sub-Saharan pest of cassava and other bush and tree crops. A number of true grasshoppers may be troublesome at times, including this species in West and Central Africa. This pest (Fig. 5.2) damages a variety of staples such as millet, cassava, bananas and plantains; crops such as pineapple, coffee, cocoa, cotton and citrus, and some ornamentals such as *Croton* and other Euphorbiaceae (Chapman *et al*., 1986). But usually most cereals are unaffected. In the drier parts of Ghana, partial defoliation of teak plantations often occurs (Wagner *et al*., 1991, in Nair, 2007). The life cycle is annual and during the dry season of 3–4 months it exists as large, diapausing eggs. Egg hatch is synchronized with the start of the rains in October or November and the nymphs, passing through 5–9 instars, take 3–4 months to mature. There may be a dry season generation in some areas. Their slow growth is possibly contingent on their sequestration of pyrrolizidine alkaloids from some of their food plants (Bernays *et al*., 1977), particularly *Chromolaema* (= *Eupatorium*) *odorata* (Compositae). Indeed, their increasing numbers have been linked to the spread of this weed, although the destruction of forest to plant more cassava is a contributory explanation. They are warningly coloured black, grey, white and yellow (bearing some resemblance to that of *Cucullia* larvae, Fig. 5.3), and move sluggishly.

The large nymphs move up to 500 m in bands, damaging some plants while missing others. Sometimes 50–100, fourth to sixth instar nymphs may be found on a single cassava bush. The adults have short- and long-winged forms, but the latter are in the minority and rarely fly more than 100 m. Mating and oviposition, from March to May, are communal affairs, with AF ~300. These activities attract the calliphorid fly *Blaesoxipha filipjevi*, which may parasitize up to 40% of the adults. This parasitoid also attacks other grasshoppers, so maintaining its population when *Zonocerus* adults are absent. Both nymphal and adult aggregations make them vulnerable to spot spaying with an appropriate insecticide, while their eggs can be raked up and left to desiccate. Their aggregative behaviour, which is found in all the outbreaking species noted above, contrasts sharply with that of an unusual, non-outbreaking grasshopper from Arizona, *Ligurotettix coquilletti*, whose population density remains stable and low. Here, territorial males defend creosote bushes (Otte and Joern, 1975). The related *Zonocerus elegans*, which also has a brachypterous morph, has a more southerly distribution, where it is a sporadic pest of cotton and other crops.

Fig. 5.2. *Zonocerus variegatus* (Acrididae) grasshopper on cassava in West Africa. Source: Wikimedia Commons, author Charles J. Sharp.

Fig. 5.3. *Cucullia* final instar larva, the shark moth on a spike of great mullein (*Verbascum thapsus*). The pattern is somewhat cryptic at a distance.

The plague grasshopper, *Aiolopus simulatrix*, attacks sorghum and other crops south of the Sahara and is notable for its nocturnal migrations. Other grasshoppers affecting the Sahel include *Oedaleus senegalensis*, *Diabolocatanops axillaris*, *Anacridium* and *Ornithacris* spp. These have been caught >100 km off the West African coast vainly migrating (Pedgley *et al*., 1995). The rice grasshoppers, *Oxya chinensis* and *O. japonica*, occur sporadically in paddies from Pakistan through to Japan and the South-East Asian islands. *Valanga nigricornis* attacks rubber in Malaysia and *Acacia* in Indonesia.

5.2.1.1(h) OTHER EXOPTERYGOTA. These include the phasmid, *Didymuria violescens*, a defoliator of Eucalyptus in the mountains of New South Wales, and *Anabrus simplex*, the Mormon cricket of Utah (Tettigoniidae). Its famous outbreak, in 1848 on the crops of the Mormon settlement, naturally engendered much prayer. Sea gulls appeared and consumed the brutes, we are told, which we may regard according to our proclivities as pest control by avian or divine intervention.

5.2.1.2 Endopterygota: Monophagous, oligophagous and polyphagous feeders (Section 2.4.1)

5.2.1.2(a) COLEOPTERA; Scarabaeidae, Dynastinae. *Oryctes rhinoceros*. Rhinoceros beetle. A major pest of coconut and oil palms in India, South-East Asia and many Pacific Islands. Adults eat the growing point, the meristematic tissue of these palm trees, namely where the nutritional value is greatest and where maximum damage to the plant results. This primary attack if repeated may be lethal, but is often followed by a secondary one from *Rhynchophorus* weevils, which is frequently so. Young adults spend a few weeks in initial development in the larval patch before flying up to this feeding site, where over a few months reproductive maturation and mating take place (Bedford, 2013). Male beetles emit an aggregation pheromone ethyl 4-methyloctanoate (E4–MO). Gravid females deposit small batches of eggs in rotted palm trunks, decayed vegetation, dead banana corms and shredded oil palm trunks in Malaysia. They then return to the palm crowns to feed again. This cycle is repeated several times for as long as 6 months, giving an AF of 50–60 eggs. This shuttling behaviour recalls that of another herbivorous scarab, *Melolontha melolontha* (Section **3.2.1.2**(**b**)).

The larvae take about 5 months to develop in decayed trunks. Both larvae and feeding adults may become infected with a specific Nudivirus (previously classified as a baculovirus), OrNV, and the fungal pathogen *Metarhizium anisopliae* var. *majus*, the variety having long spores being the most virulent, and being very effective under humid conditions (Bedford, 2013). This fungus develops and persists in the midgut epithelium and the faeces become infective to conspecific beetles after 3–9 days of infection. Diseased adults may live as long as five weeks, acting as a mobile reservoir, and spread these pathogens to either larvae or feeding adults. Late larvae, however, may survive the infection if they pupate soon enough. *Metarhizium* most frequently infests the larvae in their damp microenvironment and generally causes their death in about 3 weeks. This creates pockets of infective spores within a log, where other larvae and ovipositing females easily pick them up. Both pathogens have been used for control (Hochberg and Waage, 1991; Zelazny and Alfiler, 1991; Bedford 2013) and normally keep *Oryctes* populations in check. Synthetic E4–MO can be used to lure the adults into traps. Apart from palms killed by these scarabs, tropical storms may uproot trees, in time increasing the carrying capacity of the environment, which in turn leads to outbreaks. Other *Oryctes* spp. infesting palms are *O. monoceros* found on seedlings in the Seychelles, *O. agamemnon* on dates in Tunisia and Saudi Arabia, and *O. elegans* in the bases of date fronds in Iraq. *Scapanes australis* attacks oil palms in Papua New Guinea and *Strategus aloeus* various palms in South America.

5.2.1.2(b) COLEOPTERA; Chrysomelidae (>20,000 spp.). These are a large group of advanced, phytophagous beetles, but like weevils, have fossil ancestors dating from the Jurassic, some 155 million years ago (Labandeira, 1997). In many species, adults and larvae feed together on foliage, which is of course unusual for endopterygotes. They regurgitate a variety of enzymes, and occasionally viral particles, into their food (Fulton *et al*., 1987; Nault, 1997). Their damage is often unsightly. The larvae, lacking abdominal legs, are vulnerable to being washed off plants in heavy rain. Adults are often brightly coloured and sometimes metallic green, with red and golden reflections. This association between such bright insects and their continued activity and exposure during high insolation reduces the speed of over-heating (Willmer, 1982; Section **10.2.4.2**). Bright colours may also indicate a noxious quality; indeed some African chrysomelid beetles are so toxic that San hunters use their haemolymph as an arrow-tip poison (Godfray, 1994). In this connection these beetles have a light skeleton (11% body mass) compared to several other families of beetles (Rees, 1986; Section **8.2.2.4**(**b**)). The conjecture that they often use poisons for protection, rather than heavy skeletal armour requiring much dietary nitrogen, is worth further study.

5.2.1.2(c) COLEOPTERA; Chrysomelidae. *Leptinotarsa* (= *Doryphora*) *decemlineata*. Colorado beetles. Generally, a warm-temperate pest of potatoes. Potatoes, *Solanum tuberosum*, are the world's biggest vegetable crop (Radcliffe, 1982), being planted on ~500,000km^2 of crop lands (Leff *et al*., 2004). This most famous chrysomelid beetle may attack them to the extent that no tubers are produced. It is the predominant pest of potatoes in central and eastern North America, but also affects, on occasion, tomatoes and aubergines, and may subsist on a variety of wild *Solanum* species (Hare, 1990). The adults are yellow with longitudinal black vittae while the larvae are red and black, both being warning colour combinations. These pigments are derived from carotene in the food plants. *Leptinotarsa* spp. originally lived an untroubled life in the eastern foothills of the Rocky Mountains where they fed on wild *Solanum* spp.

When Spaniards over-ran the Andes they found that the Amerindians of the Altiplano had grown potatoes there for centuries. They brought the tubers back to Spain and the new crop then spread within Europe, a treasure worth more than gold-laden galleons. European colonists of North America brought potatoes with them and in their hazardous trek across that continent, eventually to Colorado and Nebraska. Beetle paradise occurred about 1850 (Stern *et al.*, 1959), although a little evolution was probably necessary. The colonists had left potato patches strung out eastwards across America. So the beetles started in that direction, advancing ~100 km/year to the Atlantic coast in 1874. They reached Europe in around 1920, where the potato had become the number one staple root crop, probably on a ship to Bordeaux and gradually became established in the small farms in western France. In the war-torn 1940s they spread up to the Netherlands and Germany, into Poland by 1952 and by the 1960s into USSR. Here the party newspaper *Pravda* ('The Truth') hailed them as a capitalist plot to undermine the people's agriculture. They are now regular pests in Eastern Europe, reached Turkey in 1976, and are still spreading in Asia. A long way from Colorado.

This slow march of a pest contrasts with that of the diamond-back moth (Section **5.2.1.4(a)**). In laboratory tests on second-generation beetles, the maximum duration of flight was a mere 14 minutes, giving them a range of <3 km unless blown on strong winds, and contrasting with ~22 hours for the desert locust. But in the spring, unfed, overwintered females flew, in short episodes, further than ones that had eaten potato leaves (Ferro *et al.*, 1991), a total of 4.9 km as opposed to 1.3 km. But clearly their flight capability is very limited. Swimming a few hundred metres off the coast of Brittany in August 1962, I made a collection of the adults that were in the process of uselessly drowning themselves, but from which they were saved for a noble posterity of furthering education. However, this insect is recorded crossing the Baltic Sea into Scandinavia (Wiktelius, 1981, in Pedgley *et al.*, 1995), presumably suffering great attrition.

Harcourt (1963, 1964, 1971) has investigated their biology and dynamics in Ontario, Canada, Groden and Casagrande (1986) in Michigan, USA, Ferro *et al.* (1985, 1991) in Massachusetts, USA, Tauber and Tauber (2002) in New York and Lyytinen *et al.* (2009) in Northern Europe. Adults feed and mate on potato foliage, but males provide several inseminations to fill their mate's spermatheca, and often ride her back to prevent other males having this opportunity (Boiteau, 1988). Batches of 20–60 eggs are laid on the underside of foliage (Hare, 1990). An AF of ~300 is influenced by the variety of potato attacked and presumably by female size (Section **10.2.5**). Laboratory fecundity can be greater, while Davidson and Lyon (1986) suggest a field AF of 500. In spring, fertile laboratory females that mated again laid more eggs than those that did not, a mean of 377 as opposed to 278 (Ferro *et al.*, 1991). Lyytinen *et al.* (2009) record a maximum potential fecundity (MPF) of 1500 for Russian beetles. Ferro *et al.* (1985, 1991) found multiply mated females had 95% fertility, as opposed to only 73% when mated once. But Lyytinen *et al.* (2009) estimate fertility at only ~55%. Additional egg mortality is often due to cannibalism and mud splash, and the young larvae are frequently washed from leaves during heavy rain and drown beneath the plants.

When nearing maturity, the big, gaudy larvae feed externally, eating large quantities of leaves. This often results in starvation locally. While Russian larvae (and eggs) can tolerate mildly sub-zero temperatures, in cold weather they do not eat, resulting in small beetles, low winter survival and low AF (Lyytinen *et al.*, 2009). Predators include *Coleomegilla maculata* (Coccinellidae), which eats eggs and young larvae, *Perillus bioculatus* (Pentatomidae), and in some northern states of the USA, *Lebia grandis* (Carabidae). The eulophid egg parasitoid, *Edovum puttleri*, a promising biocontrol agent, kills over 80% of the beetle's eggs under favourable conditions, but cannot overwinter in the north. Three tachinid enemies exist: two *Myiopharus* spp. on the larvae (Feener and Brown, 1997) and *Doryphorophaga doryphorae* on the pupae. In Europe, the bug and the last-named fly have been used unsuccessfully for biocontrol, probably because their effects are outstripped by the high reproductive rate of these beetles (Section **11.2.2.5**).

Bearing in mind the beetles' poor powers of redistribution, there is considerable local adaptation. In warm-temperate climates the life cycle can be completed in <1 month, so there can be three generations per year. Maximum developmental rate is at 25–33°C, depending on adaptation to cooler or warmer areas. In summer drought, however, the adults may bury themselves in the soil. In the extreme north of distribution, as in Ontario, there is only a single generation. Here the mature larvae pupate in the soil but may re-emerge to feed as non-reproducing adults. In Upstate New York the beetle is bivoltine, and a proportion of the spring generation enters diapause until the following year. Some of these beetles spend 2 or more years underground (Tauber and Tauber, 2002). Spring-generation beetles are more likely to have prolonged diapause. If food has been scarce, poor quality or senescent, they may emigrate to seek overwintering sites, a behaviour found in several phytophagous beetles. The non-migrants begin to lose water in preparation for winter diapause, which is induced by decreasing day length. In northern populations (45°N) 16 hours is critical, but it reduces to 12 hours in the south (26°N). There is much variation with latitude. At higher temperatures in the south the beetles are often insensitive to day length (Hsaio, 1981, in Hare, 1990), a neat example of a complex influence of two physical factors (Section **10.1**; Danks, 2007). Senescing foliage can also induce diapause. Diapausing adults not only lose water but also reabsorb their flight muscles.

Because the adults are long lived, their early progeny may constitute a contemporary second generation, with mother and daughter laying eggs at the same time, while their later progeny may enter pre-reproductive diapause. Thereafter, these adults pass the winter in the soil but have only moderate resistance to sub-zero temperatures (Section **10.2.2.2**), and in some years adults are often frozen to death, especially in fields. In Ontario, most beetles fly or crawl to woodlands to overwinter, where survival is greater, and densities ~200/m^2 are reported along headlands (Hunt and Tan, 2000). If the beetles can be induced to spend the winter in the fields under straw mulches, these can be removed later to affect great mortality (Milner *et al*., 1992). Beetles emerging from diapause in spring will die if they cannot obtain water for rehydration, but otherwise are capable of several short flights for a few weeks (Ferro *et al*., 1991). The related *Leptinotarsa juncta* extends only as far north as Pennsylvania (Boiteau and Coleman, 1996).

Stomach poisons kill both adult and larval beetles, preferably, of course, at an early stage of the infestation, although resistance to all insecticides, including synthetic pyrethroids, is increasing (Wierenga *et al*., 1996). Two toxins derived from *Bacillus thuringiensis* (*Bt*), the β-exotoxin ‘thuringiensin’ and a δ-endotoxin, are effective against the young larvae. Cultivars expressing high levels of Cry3A toxin are feeding deterrents. These biological insecticides appear not to have unwanted effects on insects used in biocontrol. Riddick and Barbosa (1998) found no such effects on *Coleomegilla* when fed Cry3A-infected larvae and pollen (Section **13.2.4.2**). The nematode *Neoplectana* has also been used. In tomatoes, feeding by these beetles increases the concentration of proteinase inhibitors (Section **2.4.2**). The beetle’s extreme adaptability, however, makes it likely that any such cultivars would soon become ineffective. For example, larval strains showing 1000-fold resistance to Cry3A toxins are known. In Eastern Europe, trap crops of potatoes planted 10–15 days before the main crop, comprising 2–5% of its area and placed to intercept immigrant adults, are used regularly (Hokkanen, 1991), while research continues on increasing their effectiveness (Hoy *et al*., 2000, in Tauber and Tauber, 2002). Rotating potato production is effective, but current year fields should be ≥1.5 km from last year’s fields for maximum protection (Boiteau *et al*., 2008), although a mere 500 m will affect great pest reduction (Follett *et al*., 1996). From their original rate of spread from Colorado and from their colonization of the Channel Islands from France, a distance of ~40 km, it could be that some individuals fly much further than a few kilometres, but transport on vehicles and boats must often occur. Also, because females mate before overwintering, spring migrants can lay fertile eggs. Finally, Colorado beetles are suspected of transmitting bacterial wilt of potatoes.

5.2.1.2(d) COLEOPTERA; Chrysomelidae. *Oulema* (= *Lema*) *melanopa*, *Diabrotica* beetles. Cereal leaf beetles. A widely distributed temperate and Mediterranean pest of cereals and grasses. The life cycle and habits of *Oulema* are comparable with those of Colorado beetles, but there is only a single, occasionally two, annual generations. This pest reached Michigan from Europe about 1962, and is now distributed from Ontario to Alabama in the east, and from British Columbia to Utah in the west. Although not yet established in the wheat-growing prairie states, fears that this might soon occur appear well founded (Olfert *et al*., 2004), as the climate is suitable. Both the larvae and adults can transmit Maize Chlorotic Mottle Virus and Cocksfoot Mottle Virus. The adults, who are conspicuously coloured metallic blue with red legs and some 4 mm long, emerge from a multitude of protected overwintering sites and feed on wild grasses and then on the tillers of cereals in spring. Later both they and their larvae eat the leaves of a variety of grasses and cereals, although oats are particularly affected.

Coccinellid beetles consume their eggs and larvae on the plants. *Anaphes flavipes* (Mymaridae) may kill a high proportion of the eggs and *Tetrastichus julis* (Eulophidae) attacks the larvae. As in *Lema trilineata* and tortoise beetles, these larvae cover themselves with their own frass (Wellso and Hoxie, 1988, in Danks, 2002), presumably making themselves distasteful to, and/or concealed from, predators. Like

Colorado beetles, the larvae may be dashed to the ground in rainstorms and either killed directly or eaten by carabid beetles. After 3–4 weeks of feeding they pupate in the soil. Adults of the new generation, which emerge a few weeks later, aestivate during summer, become active again in autumn, seeking out suitable overwintering sites in tussocks and plant debris, often far from the fields. *L. trilineata* is another yellow and black lined chrysomelid pest of potato foliage.

Several species of *Diabrotica* affect crops in North America and often have sub-species with different biologies and distributions. Like many flea beetles, the adults attack aerial parts of plants and the little white larvae eat their roots. They include *D. undecimpunctata*, which is divided into *D. u. howardi*, the spotted cucumber beetle and *D. u. undecimpunctata*, its western equivalent. Despite their common names they are polyphagous. They can transmit Tobacco Mosaic Virus and Southern Bean Mosaic Virus. Bacilli causing cucurbit wilt have been isolated from the guts of cucumber beetles and overwintered adults may re-infect new plants in spring. In *D. u. howardi*, there is mass spring migration from the Gulf States on southerly winds to as far north as Iowa and Nebraska in the USA, where one or two generations occur, followed by a return migration on northerly winds in early autumn; it does not diapause.

Diabrotica balteata attacks a wide variety of crops and is found mainly in southern states, while *D. virgifera*, which is mainly important on maize roots, has been considered in Section **3.2.2.1(a)**. Another small chrysomelid beetle is *Crioceris asparagi*, well known to growers of asparagus, being a conspicuous red, yellow and black. All feeding stages eat the spears, rendering them unsaleable. In the USA a reservoir population exists on wild asparagus. *Chrysomela scripta* and *Ch. tremulae* attack young poplars (= cottonwoods) across North America, especially the cultivars used in agro-forestry for biomass production, such as *Populus nigra* × *maximowiczii*. They can cause serious economic losses as their AF is high. In the south, *Ch. scripta* may have up to five generations (Coyle *et al.*, 2005). Conventional insecticides (carbaryl and chlorpyrifos) kill these leaf beetles but also their main predators, *Hippodamia convergens*, *Harmonia axyiridis* and *Coleomegilla maculata* (Coccinellidae). Soaking the propagation sticks in imidacloprid for 48 hours before planting provides protection for 10 months (Tenczar and Krischik, 2006) and conserves predators. Later, biorational insecticides, such as *Btk* and spinosad (Section **13.2.3.2**), can be used. *Galeruca tanaceti* occurs commonly in Europe on tansy, but also attacks vegetables (cabbages, beans, potatoes) and horticultural plants (dahlias). *Batophila aerata* and *B. rubi* eat *Rubus* foliage, while *Bromius obscurus*, which is parthenogenetic, feeds on grapevines. *Cerotoma trifurcata* has recently become a pest of soya beans (*Glycine max*) in northern North America, and transmits Bean Pod Mottle Virus. *Brontispa longissima* attacks coconut and sago palms from Indonesia to northern Australia, while *Ootheca bennigseni* attacks legumes in southern Africa.

Several chrysomelid beetles (Section **5.2.1.2(b)**), regurgitate viruses onto their food. One may be surprised that this has been known from at least 1924, when C.E. Smith reported the transmission of Cowpea Mosaic Virus by bean leaf beetles (Fulton *et al.*, 1987). These are all polyhedral RNA viruses that, although found in the haemolymph, fail to multiply in the vector. Usually, the beetles retain these virions for only a week or so; they rarely retain them over winter. Other potential vectors do not spread these viruses, but there is evidence that ribonuclease in the regurgitant facilitates infectivity (Gergerich *et al.*, 1986). Four viral groups exist which although common in legumes also infest several other plant families: (i) Comoviruses in legumes, curcurbits, brassicas and some Solanaceae; (ii) Tymoviruses, which rather specifically attack plants in several families; (iii) Bromoviruses, which affect some legumes; and (iv) Sobemoviruses in legumes and graminaceous plants (Fulton *et al.*, 1987).

5.2.1.2(e) COLEOPTERA; Chrysomelidae; Halticinae.

Phyllotreta spp. and other genera. Flea beetles. Cosmopolitan, generally univoltine pests of seedlings and crop plants. Several species of these small (~2 mm) beetles, which have the hind femora enlarged for jumping, may be important pests of seedlings, especially on an agricultural scale, although in the UK at least, wood pigeons are more devastating. Adults emerging in summer may cause some damage to mature broccoli and cabbage. They chew small pits in the cotyledons and young leaves. Naturally, larger plants are less affected by their attack. The larvae usually feed on roots and pupate in the soil. Many species are cosmopolitan, several are metallic green or blue, or patterned like miniature Colorado beetles. The cosmopolitan *P. cruciferae*, *P. nemorum*, the north European *P. undulata* and the American *P. striolata* and *P. ramosa*, attack brassicas. In sub-tropical regions some species attack cotton. In China, *Prodagricomela nigricollis* eats citrus, the larvae being leaf miners.

Like *Apion* weevils (Section **6.2.1.2(a)**) and many other temperate beetles, flea beetle adults overwinter in places of maximum shelter and re-migrate to the fields in spring. Here they feed on the cotyledons of beet, rape and other young brassicas (Kinoshita *et al.*, 1979; Jones and Jones, 1984; Hiiesaar *et al.*, 2009). Early sowing produces seedlings that are bigger and so better able to resist attack. But the damage caused depends not only on pest density, but also on the prevailing weather. For *P. cruciferae* in Canada, temperatures >11°C are required for growth, and >17°C for oviposition (Kinoshita *et al.*, 1979). Sunny, bright, dry weather after a cold winter (the soil is still cool) checks plant growth and favours their attack, whereas cloudy, mild weather causes slow feeding but rapid plant growth. As with butterflies (Pollard and Rothery, 1994), such a differential effect of temperature on plant and insect development is comparable to that acting in spring on trees and the overwintering eggs of both aphids and lepidopteran defoliators.

In North America, *Epitrix* has several specialized species that attack crop plants in the Solanaceae, with *E. cucumeris*, *E. subcrinita* and *E. tuberis* on potatoes, and *E. fuscula* on aubergines. *Chaetocnema confinis* eats sweet potato vines, while in Russia *C. concinna* attacks young sugar beet. One of the largest flea beetles, the metallic blue-black *Altica calybea*, is 4–5 mm long and chews numerous holes in vine leaves in the USA. In many of these beetles and several species of *Diabrotica* (Section **5.2.1.2(d)**), the larvae feed on the roots of the same plant and may transmit plant pathogens. *Atomaria linearis* (Cryptophagidae) is another small beetle that may damage sugar beet, particularly when crop rotation is discontinued (Cochrane and Thornhill, 1987). Failure of the entire crop has been recorded. Although this beetle also attacks potatoes and field peas, its numbers rarely reach pest levels on them.

5.2.1.2.(f) COLEOPTERA; Curculionidae. *Hypera* (= *Phytonomus*) *postica*. Lucerne weevil. A temperate pest of field legumes. Most weevil larvae are white and feed internally, but in this unusual species they feed on the leaves and buds of lucerne, clovers and vetches. Accordingly, they are patterned green and white and have several conspicuous pairs of pseudopodia. Although European in origin, *H. postica* reached North America ~100 years ago (Cook, 1925), and is sometimes a pest. Some females mature in autumn, lay a few egg batches and then hibernate. Others lay only in spring. There is a mixed strategy in oviposition and overwintering, but all the eggs hatch at the time when the plants are growing rapidly. They complete larval development and pupate in delicate cocoons on the plants or in litter. Second-generation adults emerge some two weeks later and proceed to aestivate. Several species of the ichneumon *Bathyplectes* parasitize the larvae. In Ontario, *B. anurus* has displaced *B. curculionis* as the main larval parasitoid. It has higher fecundity, individual searching capacity (ISC; Section **10.2.4.1**) and resists encapsulation by its host (Harcourt, 1990). As in *Apion*, a species of *Microctonus* (*aethiopoides*) (Braconidae) oviposits in the adult weevils. But when *H. postica* are infected with *Wolbachia* (Section **10.2.3.9**) the success rate of this parasitoid is reduced (Hsiao, 1996, in Batista *et al.*, 2010).

The leaf weevils *Phyllobius* and *Polydrusus* frequently defoliate young temperate trees. In the UK, *Ph. pyri* attacks young oak, beech and birch trees and may compromise forestation programmes. The larvae live in the soil.

5.2.1.3

5.2.1.3(a) HYMENOPTERA; Formicidae. *Atta*, *Acromyrmex*. Neotropical leaf-cutter ants. Numerous ant species are predatory (Section **8.2.2.4(k)**), but the Neotropical tribe Attini (Myrmicinae), containing the genera *Atta* and *Acromyrmex*, are strict fungivores. They have had an evolutionary history of some 50 million years in cultivating symbiotic ascomycete fungi, although the leaf-cutting habit is more recent. These ants are found from north Argentina though South America (*At. cephalotes*, *At. colombica*) to Panama (*Ac. octospinosus*, *Ac. echinatior*), Mexico and Texas, USA (*At. mexicana*, *At. texana*). Some species show a fine division of labour among the workers (Cherrett, personal communication). A *cutter* morph ascends a selected tree, including crop trees, on a given night and bites off leaves, while a *transporter* morph collects the leaf pieces beneath it and ferries them back to the underground nest. Unlike most leaf pests, these ants are not permanently on the foliage, they are simply nocturnal pillagers.

These ants use the leaves to culture fungi from the Lepiotaceae, on which they feed. Naturally, the fungi cultured by modern leaf-cutters are highly co-evolved. Their fungal gardens are attacked by the micro-fungus *Escovopsis*, but they cultivate a filamentous bacterium on specialized body surfaces, which produces an antibiotic inhibiting its growth (Currie *et al*., 2003). On one occasion on the Royal Society's expedition to Central Brazil in 1967, where I spent an uncomfortable but informative 8 months, leaf-cutter ants broke into a 50 kg sack of rice and removed half of it in a single night. We see that they are quite catholic in their taste! The nests may extend over 100 m^2, with several exits and entrances. The inhabitants of such large nests can defoliate a tree in a single night, and often do so.

5.2.1.3(b) SYMPHYTA AND LEPIDOPTERA: General features of caterpillars. While we considered the general functions of larvae in Section **1.2.2**, it is useful here to outline some additional features of caterpillars, the most extensive group of leaf munchers. Their name is derived from the Old French 'chatepelose', a hairy cat; but it also means a rapacious person or ravager, and is hence succinctly appropriate for these pests. Caterpillars are the larvae of either sawflies (Hymenoptera; Symphyta, mainly Tenthredinoidea, ~7000 spp.) or more often of Lepidoptera (>100,000 spp.). These taxa contain numerous munching pests of leaves and independently have developed larval forms of remarkably similar structure. Such a common solution in different groups, in this case to the needs of being a growing, biting insect feeding externally on leaves, is termed *convergent evolution*. But some such larvae are concealed and hence *endophytic* as opposed to being *exophytic*. Both groups probably radiated in the late Cretaceous in response to the expansion of the angiosperms, although some sawflies are known from the Permian. Unlike moths and butterflies, sawflies are confined largely to temperate parts of the Northern Hemisphere; *Schizocera* spp., however, can be a pest of *Manglieta conifera*, an important timber tree in Vietnam (Nair, 2007).

Eclosing caterpillars often consume much of the chorion (eggshell) as their first meal. Those that feed on tough leaves may hatch from larger eggs than those feeding on soft ones. Exophytic caterpillars have extra-abdominal legs anchoring them firmly to the leaf's edge, while allowing the anterior part of the body sufficient mobility for feeding. Larger larvae chew holes or repeated ribbons from the leaf blade to form deep excisions, but these may be blocked by toughness of the midrib or by bases of the leaf veins. It depends on the relative sizes of the leaves and the larvae. Young larvae often feed from the lower leaf surface, windowing or skeletonizing it. After some practise, one can estimate the size of a pest caterpillar by inspecting leaf damage, helping to identify the brutes when they are hidden or have pupated. Several small 'microlepidoptera' mine or roll leaves and so remain concealed. The large majority of caterpillars feed on conifers and flowering plants, but those of many footman moths (Arctiidae) feed on lichens.

Exophytic sawfly caterpillars differ from lepidopteran ones by having more than four pairs of abdominal legs, while their cuticle is usually smooth. Females slash plants to insert egg batches, hence giving the young progeny a start in life. Some species sever the resin canals, a behaviour reducing the effectiveness of the trees' defences (McCullough and Wagner, 1993, in Danks, 2002). Under drought conditions, this habit in the pine sawfly, *Neodiprion lecontei*, leads to death of both the needles and most of the eggs (Codella and Raffa, 2002). This anomalous situation needs further investigation, especially because several pine sawflies outbreak at such times, it seems to be an odd case of parental investment with negative consequences. Most diprionid sawflies carefully seal their eggs into pine needles (Knerer and Atwood, 1973). In the Tenthredinidae, several species munch the leaves of crops, particularly shrubs and trees. Many sawfly larvae are oligophagous (Price *et al*., 2005). Pupation is generally within the soil.

Lepidopteran caterpillars are distinguished from those of sawflies by having four or fewer pairs of abdominal legs (but the primitive genus *Micropteryx* has eight), each equipped with a ring of small, incurved hooks. Apart from leaf destruction from feeding, these hooks damage leaf tissue, to which the plant may respond. The group is numerous so that only the more important and interesting pest examples can be considered. The larvae of many species, unlike those of sawflies, attack a broad range of food plants, but there are several exceptions. For example, while the winter moth and *Heliothis* larvae are highly polyphagous, some species of *Archips* and *Papilio* are strict monophages.

Because the caterpillars of most larger species feed externally, they are subject to many mortality factors (Gilbert and Singer, 1975; Cornell and Hawkins, 1995). Birds are probably the main predators in all regions, but lizards are also important in warmer climes. Apart from these predators, they are often attacked by vespid wasps such as *Vespula* and *Polistes* (Section **8.2.2.4(l)**) and a great variety of hymenopteran parasitoids (Section **8.2.2.5(j)**). They may also ingest viral particles (Dwyer *et al*., 2000; Lucarotti *et al*., 2004) and the eggs of some tachinid flies (Section **8.2.2.5(h)**). Indeed, they often succumb to these enemies. Growing caterpillars frequently move away from the area of leaf on which they have been feeding, giving a dispersed pattern of herbivory, and they may even cut off partly chewed leaves. Various reasons for these behaviours have been suggested (Edwards and Wratten, 1985; Gross, 1993). Chewing may induce the plant to translocate defensive compounds to the feeding site (Section **2.4.2**) and/or predators and parasitoids are attracted to the damage, as for example the tachinid fly *Cyzenis* is to foliage damaged by winter moth larvae (Hassell, 1968). Indeed, lepidopteran larvae are the most heavily parasitized group of juvenile insects (Thompson, 1943, 1956).

Like other externally feeding insects, caterpillars are cryptically, mimetically or warningly coloured. We examine the consequences of these tactics more fully in Section **10.2.3.5**, but in *crypsis* the insect looks like a non-insect object external to it such as a leaf, a dead twig or a faecal deposit. *Disruptive pattern* disguises the insect's form intrinsically, breaking up its shape. Both function during the day when the insect is resting, reducing predation. In *mimicry*, the insect looks like, but is not, a dangerous insect or other animal species. All are forms of *natural deception* (Hinton, 1973; Trivers, 2011). *Warningly coloured* insects do not deceive: they truly advertise their dangerous quality.

Cryptic caterpillars, in addition to a shade of green matching the food plant, may be *counter shaded*, that is, darker on top and lighter below, nullifying the shadow caused by overhead illumination so they appear to be flat like a leaf. This occurs in the big larvae of many hawk moths, which in addition may have diagonal white lines on their sides resembling leaf veins. When using captive jays as predators, simply turning the larvae upside down much reduced the effectiveness of the counter shading (De Ruiter, 1956). Work by Rowland *et al*. (2008) and Rowland (2009) supports this view. In the 2008 study, counter-shaded models reduced avian predation under a wide variety of conditions. Rowland found that large larvae of the hawk moth, *Smerinthus ocellatus*, typically orientate with the darker part of their body illuminated, which reduced predation. In some hawk moth larvae that normally rest upside down, such as *Sphinx ligustri*, the counter shading is reversed (Sheppard, 1975).

In several moth families there is a subtle deceptive tactic. Pellets resembling braconid cocoons are ejected through their own cocoon wall, perhaps giving false information to potential avian predators that the food item has been destroyed by parasitoids (Hinton, 1973). In a sample of 70 species of Neotropical caterpillars, polyphagous ones were attacked by predatory ants (*Paraponera*) more often than oligophagous ones (Dyer, 1995). Dyer showed that the latter group is better defended with deterrent compounds derived from their food plants, but hairiness also gives protection. In North America, specialist parasitoids are associated with smooth larvae, generalists with hairy ones (Gross, 1993). This curious result stems from the high visibility of the latter. Unlike smooth caterpillars, hairy ones tend to be conspicuously gregarious, especially when they have caused extensive damage to trees.

For North American forest moths, many microlepidopterans are early season, concealed forms, hiding in rolled or folded leaves or mining shoots, seeds or mesophyll tissue. Such food is comparatively rich in nitrogen. By contrast, larger species tend to occur later. They feed externally and develop slowly on poor quality leaves, consuming them in quantity (White, 1976; Mattson, 1980b). However, the speed of development to pupation affects survival. Consider the following: if there were a daily rate of mortality of 5% in a batch of 100 larvae, 20 days to maturation would leave 36 of them, but if they developed in 15 days 46 would remain. Hence, natural selection should promote rapid development (Williams, 1966; namely a *Williams' effect*, Section **10.2.2.1**). But if within a species this were achieved at the expense of a smaller final size, fecundity would be less (Section **10.2.5.2**). Natural selection must optimize these opposing forces. So food quality is a factor. Such an effect occurs in the caterpillar-like larvae of *Galerucella* (Chrysomelidae) where sub-optimal willow leaves lead to slow development and higher mortality from predators (Haggstrom and Larsson, 1995). Of course, cold weather may produce the same effect (Pollard, 1979; Section **10.2.2.2**).

Caterpillars spin silk from their labial glands, using it in various ways. Swift moth larvae use it to line their earthen tunnels. Several arboreal species in the Lasiocampidae make communal webs. In some families, such as the Psychidae and Coleophoridae, the larvae construct individual cases, which protect them from harsh hygrothermal conditions and enemies. In some groups having flightless adult females, the young larvae use long silken threads to take an aerial trip. Except in butterflies, a silken cocoon normally protects the pupa.

Caterpillars sometimes cause total defoliation of a plant. When the plant is perennial, future resources are denied to it, as the leaves are the plant's factories. Growth is slowed and seed production curtailed. But in some cases a doomed plant will commit all its remaining resources to reproduction in a burst of flowering before it dies. Trees in this weakened state are vulnerable to further insect attack, notably by scolytid beetles (Section **4.2.1.2(g)**).

5.2.1.3(c) SYMPHYTA; Tenthredinoidea, Tenthredinidae. *Nematus* (= *Pteronidea*) *ribesii*. Gooseberry sawfly. A temperate pest of *Ribes*, spreading from Europe to North America. While attacking this minor fruit crop and the related white and red currants, the scale of attack is spectacular. If control is not applied, total defoliation and crop loss may well ensue. Adults emerge from the soil in late spring. Females lay eggs in rows along the main veins on the underside of leaves. The eggs swell as they mature. The black-spotted, blue-green larvae are gregarious when small and make little holes near the leaf's midrib or at its edge. They grow rapidly, disperse and consume whole leaves. Mature larvae hibernate in cocoons under litter at the soil surface or occasionally on the bushes, and pupate in spring. There may be two or even three generations per year. Unfertilized females lay only male eggs, and fertilized females lay eggs biased towards the female sex, so we suspect inbreeding (Hamilton, 1967). In some tenthredinid sawflies, however, both sexes are produced from unfertilized eggs and in a few only females develop. Indeed, parthenogenesis is common in this family (Sections **5.2.1.3(e)** and **(f)**).

5.2.1.3(d) SYMPHYTA; Tenthredinidae. *Caliroa limacina* (= *cerasi*). Pear slug sawfly. A temperate and widespread pest of top fruits in the Rosaceae. Some similar sawflies. Although they are most frequent on pear trees (*Pyrus communis*), they also attack cherries and occasionally plums and apples. Eggs are laid in a pocket formed in the slashed lower surface of the leaf (Malyshev, 1968). The larvae are slug-like and gregarious when young, skeletonizing the leaves from the upper surface. Large larvae are solitary, greenish-black and consume whole leaves. This change of being gregarious when young to solitary when old is found in the distasteful caterpillars of several pests, and also in the nymphs of *Nezara* (Section **6.3.2.1(a)**). Mature, second-generation larvae form hibernaculae in the soil, hibernate in them and pupate in spring. As with *N. ribesii*, attack may be very damaging if left unchecked. One must spray as soon as the pest is found or extensive defoliation may be caused and the next year's growth and crop yield reduced. Other *Caliroa* spp. attack oak, together with several species in *Mesoneura*, *Periclista* and *Profenusa*. *Athalia rosae* attacks crucifers in south-east Europe, while the sub-species *A. rosae ruficornis* is Japanese. *Allantus viennensis* and *A. cinctus* attack roses. Several sawflies feed on cryptogamic plants: *Heptamelus ochroleucus* bores the stems of ferns and *Nesoselandria morio* eats mosses (Smith, 2003).

5.2.1.3(e) SYMPHYTA; Tenthredinidae. *Pristiphora erichsonii*. Larch sawfly. A Eurasian and North American (Holarctic) pest of larches and tamarack. Some diprionid sawflies. The conifer larch, which is peculiarly deciduous, is an important softwood in North America, where this sawfly may cause total defoliation over wide areas. In the late nineteenth century there were severe outbreaks in several states in the north-east of North America (Turnock, 1972), and many larch woods, although being resistant to defoliation (Kulman, 1971), were almost totally destroyed. Billions of board metres of timber were lost (Ives, 1976). By 1930 this species reached the Pacific Coast, and outbreaks continue along the Canadian border. Its extended period of emergence and oviposition may lead to almost continuous defoliation: the trees have no opportunity for secondary regrowth. In Europe, however, the sawfly is sporadic and seldom a pest.

Pristiphora is parthenogenetic. The grey-green larvae are at first gregarious and later solitary. In Europe, the specific ichneumons *Mesoleius tenthredinis* and *Olesicampe benefactor* commonly attack them, but the effectiveness of the latter is compromised by another ichneumon, the hyperparasitoid *Mesochorus dimidiatus* (Turnock, 1972). Generalist parasitoids such as *Myxexoristops stolida* and *Hyalurgus lucidus* also take their toll and *Formica* ants are frequent predators. In North America, natural enemies are fewer, but biocontrol using *M. tenthredinis* and *O. benefactor* have met with some success (Ives, 1976). Some strains of the sawfly, however, resist the former by encapsulating their eggs (see Section **10.2.3.8**). The tachinid fly *Bessa harveyi* (see Section **11.4.4.1**) is often common and attacks large larvae. In Newfoundland, Canada, the masked shrew (*Sorex cinereus*) has been introduced from continental America as a biocontrol agent as it may consume >100 pupae per day. In Ontario, predation by the shrews *Sorex* and *Blarina*, and the myomorph rodents *Microtus* and *Peromyscus* (Macdonald, 1984), reaches high levels on *Neodiprion sertifer* (Holling, 1959b). In Manitoba, Canada, *Pristiphora's* dynamics are strongly affected by such pupal mortality, although the numbers of these furry predators varies widely (Ives, 1976). *Cephalcia lariciphila*, a web-spinning sawfly, also feeds on larch. *Pristiphora geniculata* eats mountain ash, *P. abietina* can be an important pest on firs in central Europe, whereas *P. rufipes* attacks red currants. *Pikonema dimmockii* and *Pi. alaskensis* attack spruce trees, the latter species often killing them.

Other sawflies, belonging to the Diprionidae, feed only on conifers and often outbreak (Price *et al.*, 2005). They are rather small, normally have gregarious larvae, and spin peculiar, double-walled cocoons. *Diprion pini* attacks pines throughout Europe and the North African coast, there being one generation in the north and two in the south. *Diprion similis* and in North America several species of *Neodiprion*, including *N. sertifer*, *N. pinetum* and *N. lecontei*, all affect pines. There may well be cryptic species among them. *Neodiprion abietis* feeds on balsam fir, but there are many strains of this species, some of which can be found on the same tree. Other strains consume white and black spruce. In Scotland, *N. sertifer*, although affecting young trees, prefers second-year foliage (Trewhella *et al.*, 2000). Thinning commercial stands of balsam fir has significant effects on the dynamics of this sawfly (Moreau *et al.*, 2006). *Neodiprion tsugae* attacks hemlock trees and *Gilpinia hercyniae* spruce. The latter sawfly was a minor pest in Europe, but on reaching North America in the 1930s it destroyed extensive tracts of forest. Several of these species host tachinid flies (*Drino* spp.), are eaten by ants (*Formica* spp.) and are killed at high densities by viruses. *Diprion pini* deters *Formica* by exuding oral droplets of resin acids from its food. Several gregarious species use secretions and synchronous jerking movements to deter parasitoids (Prop, 1960, in Gross, 1993). In some of these sawflies, larvae on the periphery are attacked by parasitoids more heavily than are central ones (Tostowaryk, 1971, in Gross, 1993). But oviposition by *D. pini* on *Pinus sylvestris* induces synomones that attract the egg parasitoid *Chrysonotomyia ruforum* (Hilker *et al.*, 2002, in Pérez *et al.*, 2013). Sawflies that feed on broad-leaved trees include *Croesus latitarsus* on birch, while *C. septentrionalis* defoliates hazel and can be damaging to small trees in nut plantations. *Pontania promixa* and *Nematus ventralis* eat willow, while *Erythraspides vitis* attacks grapevines.

5.2.1.3(f) SYMPHYTA; *Perga affinis affinis*. Eucalyptus sawfly. A south-east Australian forest pest. This family is mainly Australian and South American. The females of some species show brood care, a feature found also in the related Argidae. *Perga a. affinis* may totally defoliate some trees but is restricted to three Eucalyptus species in open forest. Females lay 50–70 eggs, often in three subequal batches on the same or on adjacent shoots. The larvae atypically lack abdominal legs and take ~1 month to hatch. At first they live gregariously in their own batch, but later all siblings make a cohesive group and form diurnal clusters around a branch, spreading out at night to consume the leaves. If disturbed, they regurgitate oils sequestered from their food plant. By the time they reach the sixth and final instar all larvae on a tree are mutually gregarious, a behaviour that suggests inbreeding (Hamilton, 1967). Indeed, the species is largely parthenogenetic although some 20% of the adults are males.

Perga a. affinis feeds throughout the winter, although of course these eucalypti retain their leaves at this time. The mature larvae spin masses of cocoons around the base of the trees just below soil level, a behaviour in marked contrast to that of most lepidopteran larvae, which disperse at this time. They diapause as prepupae, generally pupating in autumn a few weeks prior to emergence. Some small individuals, however, continue in diapause for a year or two, another case of risk spreading (Section **9.7**). *Neodiprion sertifer* (above) behaves similarly (Holling, 1959b).

5.2.1.4(a) LEPIDOPTERA; **Tineoidea; Plutellidae** (sometimes placed in the **Yponomeutidae**). *Plutella xylostella* (= *maculipennis*). Diamond-back moths. A cosmopolitan pest of brassicas and other crucifers. This worldwide pest, the most widespread of all Lepidoptera (Talekar and Shelton, 1993), reaches from Buenos Aires to Beijing and Moscow to Mombasa. But it did not become a major pest until synthetic insecticides were applied (Section **13.1.3**). Now outbreaks can lead to serious crop losses (Batista *et al*., 2010), the annual cost of trying to manage it exceeds US$4 billion, even though a diverse army of parasitoids affects it. As most cultivated brassicas were developed in Europe, this is generally thought to be its region of origin, but Kfir (1998) makes a case for South Africa having this distinction, as crucifers and the moth's parasitoids are diverse there.

Although small, diamond-backs have great migratory powers. For example, a high-level mass movement of ~3000 km took place from the Ural Mountains, through Scandinavia to Iceland within a week. Captures on a weather ship south of Iceland showed that some moths had flown ~1500 km over the sea (Johnson, 1969). In the UK, there were huge infestations in 1958 and 2000, springtime migrations from continental Europe being the main cause (Chapman *et al*., 2002). Canada, China and Japan have had similar migrations from the south. These authors used a vertically looking radar (VLR) on which the 'signatures' of migrating moths at altitudes up to ~1 km can be detected. This moth and several larger ones often migrate at 300–500 m above the ground, where warm air occurs at the nocturnal temperature inversion (Drake and Gatehouse, 1995). Despite such migrations, genetic differentiation exists between some regions such as Japan and Australia, but not between others similarly separate, such as Benin and Brazil (Pichon *et al*., 2006). These likely reflect the frequency of migratory 'flyways'.

Plutella xylostella feeds on Cruciferae: all brassicas, turnips and occasionally watercress, while in flower gardens it eats bedding plants such as stocks, wallflowers and candytuft. It also feeds on several wild crucifers (Idris and Grafius, 1996). In Ontario, early migrants tend to breed on cruciferous weeds and move to crops in later generations (Harcourt, 1957). Oviposition starts soon after mating, and is stimulated by sulfur-containing glucosinolates or by allyl isothiocyanates in the leaves. Over ~10 days or less, 100–200 eggs/female are laid, with peak oviposition being after dusk. Harcourt (1957) gives a range of 18–356 eggs (mean 159), while Sivapragasam *et al*. (1988) in Japan record a mean of 135. Eggs are laid singly or in small batches of 2–5 or more, on both leaf surfaces. Among *Brassica* crops, broccoli is especially attractive. Oilseed rape *B. napus*, another crop of choice, is grown presently over large areas.

Various *Trichogramma* and *Tetrastichus* spp. (Section **8.2.2.5(o)**), including *Te. ayyari* and *Te. sokolowaskii*, parasitize these eggs. First instar larvae mine the leaf tissue and later the little, greenish caterpillars, which are fattest in the middle, window and skeletonize the leaves. Often they are found between cauliflower and broccoli florets. Feeding stimulants are various glucosides such as sinigrin, sinalbin (Fraenkel, 1959) and glucocheirolin. They pupate in a thin cocoon under the leaf. In mild, temperate regions there may be 4–6 generations annually, according to conditions. The moths attempt to overwinter as pupae or adults, but as far north as Ontario (Harcourt, 1957), much of New York State, USA, most of the UK and Hokkaido, Japan, the species normally fails to survive winter. Some data in Harcourt (1969) indicate a male-biased sex ratio, but Idris and Grafius (1996) found female-biased sex ratios, and Sivapragasam *et al*. (1988) virtual equality. In the tropics, breeding is continuous, with a life cycle of 3–4 weeks.

In the UK, *Diadegma eucerophaga* and *D. fenestralis* (Ichneumonidae) often parasitize the larvae. But the former must overwinter in other host larvae; it does not affect pupae. A frequent alternative is *Swammerdamia lutaria*, which feeds on hawthorn (O.W. Richards, personal communication). So hedges of this tree, since they provide food for this alternative host, are worth retaining on this count alone. Formerly, they were often grubbed out to provide more crop space: now many are being replanted. In California, a comparable system exists in two cicadellid bugs and their common egg parasitoid *Anagrus* (Section **5.3.1.2(a)**). In Australia, *Diadegma semiclausum*, *Diadromus collaris* and *Cotesia* (= *Apanteles*) *plutellae* have been introduced to control diamond-backs with some success (Talekar and Shelton, 1993). In North America, *Diadegma fenestralis*, *D. insulare*, *Diadromus plutellae* and *Microplitis plutellae* are parasitoids (Harcourt, 1969; Davidson and Lyon, 1986; Idris and Grafius, 1996). In some areas, *D. insulare* cause 80–100% mortality, but the food plant species influences parasitism and the duration of development. Such effects are often linked in this way (Section **10.2.1**). In Pretoria, South Africa, where breeding is continuous, Ullyett (1947) found 18 parasitoid wasps attacking *P. xylostella*, a species of *Angitia* (Braconidae) being most numerous. In Honshu, Japan, low rates of larval parasitism from *D. collaris* occur on cabbages, but *Cotesia plutellae* is most important (Sivapragasam *et al.*, 1988). As in *Ostrinia* (Section **4.4.1.1(d)**), there is much regional variation in the parasitoid complex. It also reminds us that abundant species often host many parasitoid species. In all >135 parasitoids afflict this pest. *Plutella xylostella* is also often infected by *Wolbachia* (Section **10.2.3.9**), which can be transmitted laterally via *Diadegma* (Batista *et al.*, 2010).

Angitia spp. have been used in biocontrol programmes, but one in New Zealand nearly failed because of the hyperparasite *Eupteromalus*. In tropical highlands, (Malaysia, Java, Taiwan, the Philippines), *Diadegma semiclausum* is now an effective biocontrol agent (Dosdall *et al.*, 2012), particularly when used with *Bt* (Sivapragasam *et al.*, 1988), as traditional insecticides kill it, and probably much of the existing local parasitoid complex. *Cotesia plutellae* is more effective in the lowlands (Talekar and Shelton, 1993). In South Africa, predators such as syrphine and lacewing larvae, which normally prey on aphids, switch to consume *Plutella* larvae if their favoured food declines. After rains the fungus *Entomophthora spherosperma* may decimate them (Ullyett, 1947).

When brassicas are grown horticulturally, as they are generally in the tropics and on organic farms, making a *daily* round of inspection is an essential. An immigrant female often lays eggs on only a few adjacent plants so that the initial attack is contained. Destruction of these conspicuous plants and any cruciferous weeds will stem the problem. Alternatively, if the pest becomes numerous, the under surface of the leaves can be sprayed, preferably with a *Bt* toxin to which they are not resistant. But if one lapses vigilance until significant damage has been done and newly emerged, second-generation adults are flying everywhere, a setback is inevitable. In tropical highlands, such valuable brassicas can be grown continuously if they are irrigated. After cropping, lazy growers leave the remains of the previous crop to sprout and provide a ready source of food for these pests, which will then attack the next crop.

Heavy rain, especially in the tropics, can wash away the larvae. Indeed, infestations there tend to be more serious in the dry season, but this could be contingent on enhanced food quality (White, 1993). In Benin, populations are low during the rainy season (Bordat and Goudegnon, 1997, in Pichon *et al.*, 2006). Even in Ontario, rainfall causes considerable mortality (Harcourt, 1969). Thus, overhead irrigation in the evening, the peak period for oviposition, can been used to suppress this pest, so having a dual function. Larval success is also affected by fertilizers, while avian predation may be significant. But *Plutella* has achieved great resistance to most insecticides, even *B. thuringiensis* toxin (Caron and Myers, 2008), spinosad (Li *et al.*, 2007) and chlorantraniliprole (Ribeiro *et al.*, 2014). Parasitic nematodes have been tried, while in the laboratory Pir toxins, derived from entomopathogenic bacteria in heterorhabditid nematodes and having some sequence similarities with *Bt* δ-endotoxins (**13.2.3.2**), are toxic to them (Blackburn *et al.*, 2006). But pupae in their cocoons are hard to kill. No insect has resistance to being stamped on, so horticulturally this method and regular inspection is an effective low-tech strategy!

In cabbages, glossy-leafed varieties are resistant to attack since their surface waxes interfere with the behaviour of young larvae. Trap cropping (Section **13.2.4.4**) with yellow rocket, *Barbarea vulgaris* var. *arcuata*, also works well and mustard, *Brassica hirta*, is used regularly in India (Talekar and Shelton, 1993; Shelton and Badenes-Perez, 2006), often as an intercrop. *Plutella* populations concentrate in the alternative food plant and are heavily parasitized. Mating can be disrupted with pheromones, and yellow sticky traps have been used to monitor immigrant populations. But since this moth was not a serious pest until the advent of organic insecticides, a return to a non-chemical approach, although with modern inputs, should be the key to its successful control.

Several other *Plutella* spp. (*P. annulatella*, *P. antiphona*, *P. armoraclae* and *P. porectella*) attack brassicas but are regional and of minor importance. Related genera, considered under the Yponomeutidae by Alford (2007) do a variety of damage to plants. Species of *Argyresthia* bore buds and fruit, those of *Prays* destroy flowers, while those of *Yponomeuta* defoliate fruit trees. The adults of *Zelleria oleastrella* rest atypically and resemble twigs. Larvae of the casbearer moths (Coleophoridae) often make 'open cast' mines in leaves of fruit trees and other crops, using epidermal fragments to progressively enlarge the case.

5.2.1.4(b) LEPIDOPTERA; Pyralidae. *Nymphula depunctalis*. Rice casemoth. A pest in rice paddies. This is another small moth, being a pan-tropical pest of rice seedlings. Larvae build the leaf tips into a case and lead a semi-aquatic life in the paddy fields.

Destroying larvae when planting out, draining the fields and/or using kerosene to film the water can control them. Rice, like other graminaceous crops, is fairly resistant to pest attack although the new high-yielding varieties less so than the original, 'native' ones.

5.2.1.4(c) LEPIDOPTERA; Tortricidae. *Choristoneura fumiferana*. Spruce budmoth. A rather broad-spectrum pest of North American conifers, preferring balsam firs (*Abies balsamea*). Some other *Choristoneura* spp. This large family of mainly small moths contains several major pests. Resting adults in plan often present an elongated bell shape (see Fig. 681 in Alford, 2007). Larvae usually feed in spun or rolled leaves, wherein they pupate. The spruce budmoth is a serious pest in North America, a periodic scourge of balsam firs, less often of white, black and red spruces and other conifers. It is thus the subject of hundreds of research papers, often under the umbrella of the Canadian Forest Service. Formerly regarded as a single species, it is now separated from a western relative *C. occidentalis*, a case, as in *Anastrepha* (**6.3.1.1(n)**), in which detailed study reveals sibling species. They are now called eastern and western spruce budmoths, respectively, although *C. fumiferana* is found in Alaska (Harvey, 1996), attacking larch, hemlock spruce and several *Pinus* spp. In British Columbia, Canada, *C. biennis*, which feeds on *Picea* and *Abies*, has a 2-year cycle of numbers (Zhang and Alfaro, 2003). In eastern Canada, *C. fumiferana* has irregular periods of outbreak every 30–40 years, lasting several years with densities of large larvae reaching 4 million/ha. In the 1949–1959 outbreak some 20 million ha of forest were affected (Fig. 5.4) and several billion tonnes of timber destroyed. Such destruction in mixed boreal forests promotes an increase in the numbers of broad-leaved trees such as *Populus tremuloides* (Regniere and Nealis, 2008). In the last episode in 1982, some 30,000 km^2 were sprayed from the air, doubtlessly with devastating attrition to the total insect fauna. Classic works are those of Wellington (1948, 1957, 1960), Morris and Miller (1954), Miller (1959, 1960), Morris (1963) and Holling (1973). See also Andrewartha and Birch (1954, 1984), Harvey (1985, 1996) and Boulanger and Arsenault (2004). Royama (1984, 2001) has details of their dynamics. Rainey (1989) gives an insightful review of their spectacular migrations.

In *C. fumiferana*, the eggs are laid in summer in several masses on the needles in the crown. The first larval instars may or may not migrate, a process facilitated by their position on the tree, and if they do so, like winter moths (Section **5.2.1.4(g)**), they employ silken threads. The proportion migrating is greater when the weather is suitable: sunny with light to moderate winds. Convection currents at such times can lift them and hence maximize their spread (Gatehouse, 1997). These larvae do

Fig. 5.4. Destruction of balsam firs by the tortrix moth *Choristoneura* in New Brunswick. Source: Steven Katovich, USDA Forest Service, Bugwood.org.

not feed but spin silken hibernaculae in places of favourable humidity, especially within old staminate flower cups, in which they pass winter diapause. Very cold winters kill them since their body fluids freeze as their natural cold hardiness, which depends on a high concentration of glycerol antifreeze in the haemolymph (Danks, 1978), is exceeded. Widely fluctuating winter temperatures, including periods just above zero, are also destructive, but a good early snow cover protects them. Interestingly, larvae from larger eggs are more resistant than those from smaller ones (Harvey, 1985). Indeed, there is a northward cline of increasing egg size. In *C. occidentalis*, neonate larvae emerging from peripheral egg batches seek more central overwintering niches, spin hibernaculae and moult into the second instar. Since their only food resource is that provided in the egg, the cooler micro-environment in autumn, and the more sheltered ones in winter, promote survival (Nealis and Regniere, 2016).

In *C. fumiferana* surviving second instars emerge in spring, many migrating on silk. Since they have not fed they are lighter than first instars. There is some evidence of their moving 35 km by this means, which is likely to have greater success where there are dense stands of their food plants. Note that larval dispersal can result in a less clumped distribution. This dispersive behaviour in two successive instars is odd but forms the major loss to population (Morris and Miller, 1954). Andrewartha and Birch (1984) suggest that since the prevailing winds are different in summer and spring, this strategy improves environmental scanning (q.v.). Having migrated successfully, or remained on their natal tree, they bore vegetative buds or feed on new needles, but also relish the pollen cones of balsam fir. Late frosts in May can kill these buds and so reduce the supply of preferred food. Food selection is larval not maternal (Section **10.2.4.7**). Initially, larvae live gregariously, tying shoots together with silk and selecting elevated places where sunshine penetrates. Their orientation behaviour is important both in relation to defoliation and as a mechanism maintaining hygrothermal balance (Section **10.1.1**). They generally pupate *in situ*, emerging in late June and July. Adult females are usually grey and mottled, or brown, the result of a sex-linked gene (Stehr, 1955, in Morris, 1963).

When frontal systems approach, the moths leave the canopy and ascend up to ~1000 m in convectional storms (Henson, 1951), flying at an air speed of about 7 km/h. Interestingly, ionization of the air as in storms, increases the migratory capacity of the blow fly *Phaenicia* (= *Lucilia*) *sericata* (Maw, 1965) and so is possibly a factor in this case. Winds can carry these moths at up to 50 km/h, so they may cover 200–300 km in a single night. Rainey (1989) reports vast masses of 10^{10} migrants covering an area of 10,000 km^2. This mass movement causes considerable gene flow and all populations from Alaska, USA, to Newfoundland, Canada, are 'generally homogeneous' genetically (Harvey, 1996). But wind convergence can cause great concentrations on areas formerly having few moths, resulting in juvenile densities that far outstrip the depredations of resident predators and parasitoids. In one stand of balsam fir, Morris and Miller (1954) estimated >500 eggs/m^2 being laid by immigrants in addition to ~60/m^2 eggs expected from residents. Similar migrations occur in *Zeiraphera diniana*, the next major tortricid pest to be considered.

Both sexes fly, so the species is further unusual in having three redistributive stages: two larval instars and the adults. Large females often migrate *after* having laid many eggs, so not conforming to the oogenesis-flight syndrome (Section **10.2.4.1**). As in *Tipula paludosa* (Section **3.2.1.2(f)**), Wellington showed that if females came from well-fed larvae, they were heavy and highly fecund but poor fliers and might lay >50% of their eggs at the emergence site and others elsewhere, should they find suitable food. Mated females lay several clusters of 40–70 eggs in tree crowns. AF rarely exceeds 200, and while increased by multiple matings, this rarely occurs (Outram, 1971). AF is 170–195 eggs/female when larvae have eaten good food (young leaves, male cones) in uncrowded conditions, much less on poor food (old leaves) when crowded, when AF may be <80 (Morris and Miller, 1954), a good example of density-dependent reduction in natality. It can be compared to similar effects in blow flies on small carcasses (Section **10.2.5.2**) and in dense clones of aphids. In *C. pinus*, AF averaged 62 during population increase but only 43 in decreasing populations (Foltz, 1972). Natality would also be greatly reduced if, as above, moths disperse during egg laying but fail to find a new oviposition site. In New Brunswick, Canada, the percentage of eggs laid by *C. fumiferana* was 70–86% of the total carried (Thomas *et al.*, 1980). In culture, egg batches have only 13–19 eggs and AF 90–230 in once-mated females (Nealis and Regniere, 2004). Batch size is positively correlated with AF ($P = 0.002$), but fecundity and egg size is correlated with several forms of the maternal X-chromosome (Campbell, 1962, in Ginzburg and Taneyhill, 1994).

Apart from ~7% predation on the egg clusters (Morris, 1963), spiders and birds such as the bay-breasted warbler and the olive-backed thrush consume the budmoth throughout. Baculoviruses may infect them, but not at a level to affect their dynamics materially (Lucarotti *et al.*, 2004). Microsporidian parasites can be transmitted via the ovary. The diminutive chalcidoid wasp *Trichogramma minutum* (Section **8.2.2.5(o)**) commonly parasitizes the eggs during outbreaks, an event more probable in warm, rain-free periods that allow it more searching time (Bourchier and Smith, 1996). The braconid wasp *Apanteles fumiferanae* and the ichneumon *Glypta fumiferanae* (Miller, 1960; Morris, 1963) attack early instar larvae and so overwinter and migrate within them. In spring two ichneumons, *Synetaeris* spp. and *Horogenes conodor*, afflict third and fourth instars and a diversity of dipteran and hymenopteran parasitoids have been recorded from large larvae. These include *Meteorus trachynotus* (Braconidae) and *Tranosema rostrale* (Ichneumonidae), the latter employing a polydnavirus (Section **8.2.2.5(k)**) to combat its host's defences. Parasitism by *M. trachynotus* is low at outbreak densities of the moth, increasing only when they decline. Tachinid flies such as *Lypha setifacies*, *Phryxe pecosensis* and *Winthemia amoena*, also attack big larvae. Again, percentage parasitism from them is low at high host density. Two polyphagous ichneumons, *Ephialtes* (= *Apecthis*) *ontario* and *Itoplectis conquisitor*, attack the pupae, which sometimes show female-biased mortality. Overall, parasitoids kill a decreasing fraction of the moth (*inverse density dependence*; Section **11.4.4.2**) during outbreaks and so fail to maintain top-down control (Morris, 1963). In fact, larval instars 2–6 have a higher rate of survival in dense infestations (34%) than in moderate ones (6%) (Morris, 1957). Ultimately, the increasing proportion of large larvae to their resources leads to defoliation. But apart from death from starvation, decreasing food quality and quantity result in smaller, more dispersive and less fecund adults, thus reducing dense local populations.

Indeed, widespread defoliation and the death of countless trees generally occur only after several successive years of attack when the weather has been dry (Holling, 1973) and is more likely to occur in mature forests where balsam fir flowers every year, instead of its normal biennial pattern. But the worst effects are seen frequently in stands on poor soils or in those that have been attacked by bark beetles (Section **4.2.1.2(h)**). In all cases of outbreak, enhanced nitrogen levels in the aerial parts of the trees may be a primary cause (White, 1993), although AF is highest when outbreaks are beginning or ending and defoliation is low (Nealis and Regniere, 2004). In their work, defoliation during larval development explained 83% of variation in the reduction of AF of resulting females.

Control problems, as for locusts, are due to spatial scale and accessibility. Look at a good map of Canada and note the many large areas between the roads. While there are logging roads, formerly wide-scale aerial spraying was deployed (Prebble, 1975). Also, the pests are in the tree crowns. For the last 40 years, mating disruption with synthetic sex pheromones has been explored and developed (Rhainds *et al.*, 2012). For example, the pheromone E:Z-11 tetradecenal can be applied from the air in micro-capsules, fibres or flakes. While this moth has traits such as univoltinism and a brief emergence period favouring such control, mating disruption should be applied at low population densities. This might well prevent outbreaks, as the method is more efficient at such times (Cardé and Minks, 1995). Early intervention is key. In addition, aerial sprays of *Btk* (Section **13.2.3.2**) are preventative but much less specific. A related point is that male survival is merely 0.67/day (Sanders, 1983, in Rhainds *et al.*, 2012).

We saw above that attacks are strongly periodic, the moth being scarce between episodes. Outbreak density is over three orders of magnitude greater than in rarity (Morris, 1963). Such population behaviour is predicted in a chaotic model by Vandermeer (1982); however, in natural populations of this species migration is a major feature, one that is absent in his model. Also, such occasional high density has little insurance value for survival (den Boer, 1968). Because budmoth damage reduces the growth rate of the trees during outbreaks, the growth rings are close together for the several years. A dendrological investigation shows that past attacks started in 1770, 1806, 1878, 1912 and 1946, giving evidence that populations cycle every ~35 years (Royama, 1984; Boulanger and Arsenault, 2004), although some peaks are missing. A recent outbreak began in some areas in 1983, and lasted for ~10 years (Williams and Liebhold, 2000; Nealis and Regniere, 2004). These cycles are much longer than those of other outbreaking forest moths, whose periods are frequently in the range 7–11 years or less (Sanders *et al.*, 1985; Myers, 1988, 1998; Berryman, 1996).

Apart from *C. occidentalis* and *C. biennis*, other *Choristoneura* include *C. pinus* on jack pine and *C. conflictana* on aspen. *Choristoneura* (= *Cacoecia*) *murinana* is the European fir budmoth. While *C. pinus* may outbreak, its food plant produces few male cones in a subsequent year. This lack of preferred food, coupled with the lagged, top-down effect of enemies terminates the outbreak (Regniere and Nealis, 2008). As in winter moths, larval emigration is induced by insufficient food (Nealis and Lomic, 1994). *Choristoneura rosaceana* can be a major pest of apples and other top fruits (Hsu *et al.*, 2009), particularly because of its effective migratory powers.

5.2.1.4(d) LEPIDOPTERA; Tortricidae. ***Zeiraphera diniana*** **(=** ***griseana*****).** The larch budmoth. A strongly cyclical pest of larches and a few evergreen conifers, in the European Alps and Pyrenees. This moth has been researched intensively by foresters and entomologists for over a century and can be regarded as the European equivalent of the preceding species. Like *C. fumiferana* it has outbreaks, but these are more frequent, having a period of 8–9 years (8.24 ± 0.27 standard error; Berryman, 1996). It is also univoltine, but overwinters as small batches of eggs under lichens on the branches of its food plants which include *Larix decidua* (generally), *L. leptoleptis* in Britain (Day, 1984) and *L. russica* and *L. gmelini* in Russia. Outbreaks have also occurred on *Pinus* and *Picea* spp. across Europe (Baltensweiler *et al.*, 1977). The eggs are very resistant to low temperatures. Alpine larvae hatch in May, feed on the new foliage at night and mature at the end of June. Later instars spin communal webs in which they rest during the day. During outbreaks, competition for food becomes critical and, as in *C. fumiferana*, larvae are often forced to leave the trees before being fully fed, leading to lower pupal weights, reduced survival and AF. They pupate in litter and emerge in July.

Large, well-fed females, avoiding defoliated trees, lay ~130–150 eggs over a 2- to 3-week period (Baltensweiler, 1964), but as few as 20 if they have been starved. Defoliated trees produce new leaves in August, but these may be killed by early frosts and the tree may die. If not, it produces shorter needles for the next year or two, which, as in *C. fumiferana*, have reduced nutritional value (Turchin, 2003), a density-dependent, bottom-up factor (Sections **9.8** and **12.2**) with a *lag effect*. Time lags are regarded as drivers of population cyclicity (Section **11.5.1**).

Larvae have two, genetically based colour forms, a blackish one found mainly on larch, and a light orange one on conifers such as *Pinus cembra* (Baltensweiler, 1993). The polymorphism is also modified by temperature, with more dark morphs in the final instar when it is cooler. As in other insects, dark forms pick up heat from insolation more efficiently than light ones, while alpine environments, although cool, have high levels of insolation (Section **2.2.2.2**). Dark morphs hatch early, coincident with larch bud burst, so increasing survival. The polymorphism is expressed on two time scales: (i) within generations, allowing phenotypic plasticity to adapt to prevailing temperature; and (ii) between generations, where nutritional stress selects subsequently for a different genetic structure (Baltensweiler *et al.*, 1977). Outbreaks are also driven by assortative mating between dark morphs (Baltensweiler, 1993). As in winter moths, a match in hatching and bud burst times is critical for larval survival (Danks, 2007), and so their dynamics. Turchin (2003, pp. 213–238) reviews hypotheses explaining the moth's marked cyclicity, concluding that while variation in food quality has explanatory value, a tritrophic model including mortality from parasitoids gives a better fit.

Indeed, the larvae host a battery of parasitic wasps, 76 species being recorded from the Swiss Engadine alone. There is a eulophid complex (*Sympiesis punctifrons*, *Dicladocerus westwoodii* and *Elachertus argyssa*) about halfway through larval development and the ichneumons *Phytodietus griseanae*, *Diadegma patens* and *Triclistus* spp. later on. Parasitism is greatest just *after* peak densities and best regarded as density dependence (Section **10.2.3.7**) with a time lag. Probably budmoth numbers *drive those of its parasitoids*, but as is often the case, parasitism has been underestimated in previous work (Berryman, 1996; Turchin, 2003; Section **11.3.1**), since many deaths from this cause remain unrecorded (Kidd and Jervis, 1996; Section **11.4.2**). Baculoviral disease terminated the moth's outbreak in the 1950s, but has not re-appeared. Other pathogens are *Entomopoxvirus* spp. and the microsporideans *Octosporea* and *Telohania*.

Outbreaks, measured by the defoliation they cause, move as waves through the metapopulation of this moth. Bjornstad *et al.* (2002) show that peaks of population, originating in the Alps Maritimes, move along the alpine larch forests towards Austria, a distance of ~900 km, at a rate of ~220 km annually. Fisher (1937) modelled such wave movements, which accord with Thompson's theory (Section **11.2.2.1**) and suggests populations move out in successive generations after environmental degradation. A similar dynamic occurs in Canadian lynx cycles (Moran, 1953; Pielou, 1981), *Hyblaea* in India (Section **5.2.1.4(k)**), and the recent spread of two *Phyllonorycter* leaf miners in the UK (Section **12.3.4.3**). Migrations of both *Z. diniana* and its major parasitoid may be involved in the wave, and so peak numbers are not synchronous as they seem to be in European winter moths (Section **5.2.1.4(g)**), but sequential with distance.

Zeiraphera canadensis attacks white spruce in north-eastern North America. Like *Z. diniana*, it overwinters as diapausing eggs that hatch at bud burst. Young larvae mine the needles; later they destroy terminal shoots and suppress apical dominance. The entomopathogenic nematode, *Steinernema*, has been used against it. Other tortrix moths to note are *Archips argyrospilus*, the fruit tree leaf roller, which is sometimes an important orchard pest along the Pacific West Coast. Further species are *A. fervidana* and *A. semiferana* on oak, while *A. micaceana* attacks *Acacia mangium* seedlings in Thailand (Nair, 2007). *Homona magnanima* feeds on tea.

5.2.1.4(e) LEPIDOPTERA; Lasiocampidae.

Malacosoma americanum, *M. disstria*, *M. nuesstria* and other *Malacosoma* spp. Tent caterpillars and lackey moths spinning communal webs. Some other lasiocampid moths. *Malacosoma americanum* eats apple and wild cherry foliage in eastern North America, while *M. disstria* is a forest species that often attacks aspen in Canadian parks. In early summer, *M. americanum* deposits helical batches of 150–250 eggs, which are encased in a protective material and may girdle a twig. These develop into pharate larvae that do not hatch until spring. Then they spin a communal web (Fig. 5.5), often around a small forked branch, an example of co-operation and food selection by siblings. Despite this incipient sociality, the hatching date is variable and under genetic influence. Different groups enclose at different times, spreading risk in a harsh, unpredictable environment. When sunny the web produces a microclimate several degrees above ambient and protects them from many enemies (Joos *et al.*, 1988; Frid and Myers, 2002). The brightly coloured larvae forage out from their retreat during the day leaving a silken trail, and eat buds if the leaves have not yet opened. They extend the web as they grow; finally it may be 70 cm long. A defoliated area develops around the web, making the ensemble conspicuous. *Malacosoma constrictum* and *M. tigris* build new tents at each moult, while *M. disstria* employs only a silken

Fig. 5.5. A communal web spun by *Lymantria* sp.

mat (Fitzgerald and Willer, 1983). Larvae mature in June, leave the tree and each other and spin powdery white cocoons in sheltered places. Adults are short lived but even so are migratory (Brown, 1965), who records a rapid, ~500 km migration of *M. disstria* on a cold front. Females are rather larger and fatter than males.

In orchards, winter washes (Section **13.3.3.2**) were used to kill the eggs, but have now been replaced. In parkland, *M. disstria* feeds on various willows, aspens and maples, and insectivorous birds fly in to feed on them, operating as density-dependent predators with an aggregative response (Parry *et al*., 1997; Section **10.2.3.9**). *Telenomus clisiocampae* (Scelionidae), *Ooencyrtus clisiocampae* (Encyrtidae) and *Baryscapus malacosomae* (Eulophidae) afflict the egg clusters (Williams and Langor, 2011), but the 'egg bands' are partly or wholly covered with a foamy secretion that reduces parasitism. The tachinid flies *Leschenaultia exul*, *Carcelia malacosomae* and *Patelloa pachypyga* parasitize the larvae, and the sarcophagid fly *Arachnidomyia aldrichi* larviposits on the cocoons (Roland and Taylor, 1997). The cyclical dynamics of *M. californicum pluviale* are driven by the incidence of nucleo-polyhedrovirus (NPV), which devastates them at high density. Death from the NPV is more rapid in warm weather, a further example of interaction between a physical and a biotic factor (Section **10.1**; Frid and Myers, 2002).

Early larvae of the pan-European *M. neustria* also build a communal web and have a similar life cycle to the above species. They retreat inside the web to moult. This lackey has a broad spectrum of food plants and apart from eating foliage in the Rosaceae (apple, plum, sloe, cherry and hawthorn) attack oak, elm, birch and willow. Mature larvae pupate in double-walled cocoons (cf. diprionid sawflies, Section **5.2.1.3(e)**) often spun between leaves (Alford, 2007). Other American species are *M. constricta*, which eats oaks, red alder and orchard trees, and the West Coast species *M. californicum pluviale*, which feeds on similar food. In some *Malacosoma* only some individuals in an egg mass eclose in any year, a risk-spreading strategy like that of *Aedes aegypti* (Section **7.3.2.4(d)**). Annual changes in individual quality are known in several *Malacosoma* spp. For *M. pluviale*, parental quality resulting from variation in their nutrition, namely an inherited environmental effect (Section **11.2.3**), is largely responsible (Wellington, 1964). The pine lappet moth, *Dendrolimus pini*, which has probably spread from continental Europe, has recently become a sporadic pest of pines in Scotland, while another lappet, *Gastropacha quercifolia*, is a minor pest of top fruits.

5.2.1.4(f) LEPIDOPTERA; Lymantriidae (= Liparidae). *Lymantria* (= *Porthetria*, = *Ocneria*, = *Liparis*) *dispar* (Gypsy moths). A broad-spectrum pest of Palaearctic and Nearctic hardwood forests. This is a widespread pest of forest trees in parts of continental Eurasia, outbreaks in Bulgaria, Romania and areas of former Yugoslavia (Berryman, 1988, 1996), occupying the region 30–60°N (Keena *et al*., 2008). In North America, it is very damaging to hardwoods and occasionally to fruit trees in the Eastern States. One can contrast the gypsy with *Choristoneura* and *Zeiraphera*, which are essentially pests of conifers. But it has several ecological similarities to *Orgyia antiqua*, the vapourer moth and the winter moth, the latter being a taxonomically unrelated species. All have, unlike many moths, the following characteristics: polyphagous caterpillars, strong sexual dimorphism with females that fly poorly or not at all, and young larvae that can migrate on long silken threads. The long hair on *L. dispar* and *O. antiqua* larvae should make this form of dispersal more effective (Taylor and Reling, 1986a), although Bell *et al*. (2005) regard such an effect as trivial.

The gypsy moth was introduced into Massachusetts in 1869 (Walter *et al*., 2015) for trials on commercial silk production, one of several European moths to reach North America (Niemela and Mattson, 1996), but inevitably escaped. It has spread slowly (4 km/year) but inexorably to the west and south, affecting much of North America from Wisconsin to the Appalachians, and although it has several enemies, efforts to contain it continue. This rate contrasts with the ability of the young larvae to migrate up to 50 km, although Mason and McManus (1981, in Roff, 1990) estimate a *mean* distance of only a few hundred metres. This parameter must be considered against the fact that >12,000 larvae may disperse from a hectare of forest over the 10-day hatching period (Taylor and Reling, 1986a). But it is possible that while isolated larvae survive to adulthood, they fail to find mates (an *Allee effect*; Section **10.2.2.4**), thus explaining its slow spread (but see below). An Asian race, originally confined to northern Japan and other parts of the Far East, arrived in Vancouver, Canada, in 1991. In Eurasia, the percentage of volant females varies from >70% in parts of China and Japan to 0% in Austria, France and Switzerland. In Germany, flight ability is trimorphic with significant proportions of fliers, gliders and flightless females (Keena *et al*., 2008). Surprisingly, while a female's weight is related to her MPF, her ability to fly is not. Low powers of dispersal are known in the weakly flying *Callimorpha dominula* (Ford, 1955, 1975). Taylor and Reling (1986a, b), however, record many first instar larvae at altitudes >1 km above an outbreaking population, and suggest that individuals may be able to adjust their flight duration by changing the length of their silken thread, as some aphids do by other means (Kennedy and Booth, 1963a and b).

The gypsy was introduced into Britain from continental Europe in about 1800, and for a time was locally common, but by contrast to North America, it is presently infrequent and never a pest. Such are the mysteries of population ecology that we must solve. Unfortunately, it is a difficult study in rare insects, although of considerable theoretical importance (but see Eickwort, 1977; Ittyeipe and Taffe, 1982; Thomas, 1995; Garraway *et al*., 2008), desirable as such work is (Jayasingh and Freeman, 1980; Hanski, 1990; Hunter, 1991).

Eggs are the overwintering stage and deposited in a single mass of up to 900 covered by scales from the tip of the female's abdomen, presumably as a form of protection. In Higashiura's study (below), birds ate the eggs only when other foods were scarce (Higashiura, 1989). The minute, encyrtid parasitoid *Ooencyrtus kuvanae*, and less frequently *Anastatus disparis* (Eupelmidae), attack these eggs. *Ooencyrtus*' ovipositor can reach only surface eggs in the mass, so, because of surface/volume effects (Section **1.2**), potentially a larger proportion (up to 40%) can be parasitized in small masses than in large ones (Weseloh, 1972; Elkinton and Liebhold, 1990). Egg mortality is therefore inversely density dependent (Lessells, 1985; Section **11.4.4.2**) since the innermost eggs are in a refuge formed by their siblings: a case of involuntary altruism, or as Hamilton (1971) described it, 'a selfish herd', here a static one (Section **10.2.3.9**). Also, these late-laid peripheral eggs contain less yolk than early laid ones (Leonard, 1970), so the vulnerable ones are given less investment. Higashiura (1989) uncovered another interesting feature about the eggs in Japanese gypsies. In cool temperate Hokkaido, Japan, where there is regularly deep snow, many egg masses are laid (in summer) below what becomes the winter snow level. Over several years, predation varied between 4% and 71%. In years of high predation (by nuthatches and titmice; for the latter the American name 'chickadee' is fitting and preferable: they are not even mice!), eggs under the snow had significantly higher survival than those above it. Because females often show little discrimination as to where they oviposit, the egg masses are sometimes transported (Sharov *et al*., 1996), for example, on logs, fencing posts and even vehicles, producing small isolates that can be far ahead of the advancing population front.

The gypsy attacks >500 tree species, although few of them seriously, and the density of egg *masses* often exceeds 5000/ha, while Taylor and Reling record 12,500/ha. Gypsies are nominally polyphagous but there is a strong preference for particular tree species. On Hokkaido, Japan, in a forest plot with 11 tree species, >99% of the eggs were on *Populus sieboldii* and *Betula platyphylla* (Higashiura, 1987). In Quebec, it prefers *Quercus rubra*, *P. grandidentata*, *Ostrya virginiana*, *Acer saccharum* and *Amelanchier* spp. (Lechowicz and Jobin, 1983), who use an electivity index, E*, to estimate its preferences. But these may be different in other parts of North America, and may well be a result of local adaptation. Note that poplars produce fresh leaves throughout the summer, while oaks do not. Larvae in culture also survive on soya bean leaves. The hairy, blue, black and red larvae feed for ~40 days or more according to food and physical conditions. Laboratory studies (Barbosa *et al*., 1986) show that survival is high on various oaks. They normally feed at night and when older, like the moth *Melipotis* (Section **5.2.1.4(g)**), they hide under refugia such as flakes of bark and even beneath the tree during the day (Campbell and Sloan, 1976). At high population intensities, however, they feed continuously in the canopy, although in brief bouts (Lance *et al*., 1987).

In North America, *Apanteles* (= *Cotesia*) *melanoscelus*, *A. porthetriae* and *Rogas lymantriae* (Braconidae) parasitize young larvae. *Glyptapanteles flavicoxis* was introduced from India in 1981. Food plant species affects the survival of *A. melanoscelus* (Warren *et al*., 1992). The ichneumon, *Phobocampe disparis*, and two oligophagous tachinid flies, *Blepharipa scutellata* (= *pratensis*) and *Parasetigena agilis*, attack older larvae. A third such fly, the widespread and polyphagous *Compsilura concinnata*, none the less often causes high larval mortality (Elkinton and Liebhold, 1990), more particularly at low levels in the trees (Weseloh, 1982). In Eastern Europe, these tachinid flies and polyphagous species of *Blondelia*, *Exorista*, *Drino* and *Zenillia* attack the gypsy (Sisojevic, 1975; Section **8.2.2.5(h)**).

Survivors pupate in silken cocoons spun in chinks in the bark, under moss, in leaf litter or in other suitable refuges. *Brachymera intermedia* (Chalcididae) attack the pupae, although they can spin within their cocoons to dislodge it (Cole, 1959, in Gross, 1993). Even so, higher proportions succumb in populations at high density. *Coccygmimus turionella* and *Sturmia scutellata* are, respectively, ichneumonid and tachinid pupal parasitoids. Outbreaks of gypsies often occur in forests lacking an understory and herbs to support alternative hosts for these various parasitoids (van Emden and Williams, 1974). In North America, the mouse *Peromyscus leucopus* and several other small mammals (Section **5.2.1.3(e)**) eat the pupae and mature larvae. Even at low densities of *L. dispar*, Campbell and Sloan (1976) found ~70% such mortality, with females (larger than males) being more vulnerable. High numbers of *P. leucopus* are associated with an abundance of acorns, which in turn puts predatory pressure on the moths. This system may be responsible for the synchronous outbreaks of the gypsy over wide areas (Elkinton *et al*., 1996) when the numbers of this rodent decline. Although avian insectivores feed on the caterpillars when hungry, they manifestly prefer less hairy food in North America, but apparently not so in Japan (Furuta, 1976, in Campbell and Sloan, 1976).

Paecilomyces farinosus (Fungi Imperfecti) occurs on egg masses attacked by *O. kuwanai*, but in the laboratory does not infect healthy eggs. However, another fungus, *Entomophthora maimaiga* (Zygomycetes: Entomophthorales), has been used for biocontrol. Large resting spores from infested larvae wash off the trees and tend to accumulate around their boles (Weseloh and Andreadis, 2002), where the larvae often pupate (Campbell and Sloan, 1976). They may persist for up to 10 years. Some of these spores germinate in spring, producing numerous, smaller, airborne conidiospores, which may infect arboreal larvae. This fungal pathogen thus bridges periods of abundance and scarcity of its host, a further case of risk spreading, but may not suppress gypsy moth numbers consistently (Ellington *et al*., 1996). Partial suppression of larval gypsy and other lymantriid moths (*Orgyia*) has been obtained using NPV baculoviruses (Lucarotti *et al*., 2004), which Doane (1970) and Dwyer *et al*. (2000) have implicated in the collapse of gypsy numbers. Additionally, high tannin levels in food reduce larval susceptibility to them (Schultz, 1988).

Nubile females, typically perching on tree trunks, call males by emitting a sexual pheromone. Trials in the 1970s using the synthetic pheromone ‘Disparlure’ showed that only a few per cent of the marked males were recaptured, making the method good only for monitoring population size, not for reduction. However, mating disruption techniques show greater promise for control and are now used throughout 230,000ha in the USA (Witzgall *et al*., 2008). *Bacillus thuringiensis* var. *kurstaki* (*Btk*) has been used in parkland (Webb *et al*., 1991). While attempts at eradication have been made, for example in Michigan (Myers *et al*., 1998), they were only partially successful and temporary. A more practical method is to define a 100 km-wide barrier zone along the advancing front, and eliminate the isolated colonies it contains (Liebhold and Tobin, 2008). Such isolates are still in the grip of Allee dynamics (Section **10.2.3.7**). For good bibliographies, see Elkinton *et al*. (1996), Dwyer *et al*. (2000) and Keena *et al*. (2008).

Orygia antiqua is a European lymantriid moth with apterous females, hence showing convergent evolution to the next species, the winter moth, which is in quite a different family (Hunter, 1995). The females lack flight muscles, and the ovaries extend into the thorax (Sattler, 1991), as in ovipositing *Apion* (Section **6.2.1.2(a)**). The orange/brown males fly during the day in summer and mate with females on their cocoons. As in *Lymantria*, a single batch of several hundred eggs is laid and the hairy little larvae, which are polyphagous, may disperse on silken threads. North American species are *O. vetusta*, *O. pseudotsugata* (Mason, 1974, 1976, 1978) and *O. leucostigma*, the white-marked tussock moth (Harrison, 1994). There was an outbreak of the latter in 1998 in Nova Scotia, Canada, but it had virtually disappeared by 2001. Its decline was associated with a high incidence of both singly imbedded NPV and the fungus *Entomophthora aulicae*. In the South-East Asian *O. thyellina*, females are winged or apterous, the latter laying fewer, larger eggs (Sato, 1977, in Zera and Denno, 1997). It became an urban pest in Auckland, New Zealand, but was eradicated using aerial applications of *Btk* (Section **13.2.3.2**). A related moth, *Teia anartoides*, an Australian native, is also invasive in Auckland and controlled similarly. Two other such moths, *Lymantria mathura*, the pink gypsy, and *Calliteara cerigoides*, defoliate *Shorea* spp. timber trees in parts of India and South-East Asia (Nair, 2007). *Lymantria monacha* is associated mainly with conifers in Europe, while *E. albescens*, *L. umbrosa*, and *L. postalba* are found in Japan (Keena *et al.*, 2008). *Lymantria ninayi* occurs on *Pinus patula* in New Guinea.

5.2.1.4(g) LEPIDOPTERA; Geometridae. *Operophtera brumata*. Winter moths. Broad-spectrum pests of European and North American forests and orchards. Rather unusually, winter moths are pests of forests and orchards and even moorlands. This stems from their widely polyphagous habits. Their population dynamics have been well studied in Europe and North America, so that they are a fitting example here. After Varley's original work at Oxford (below), several workers investigated populations in eastern Canada in forest (Embree, 1991) and orchard situations (MacPhee *et al.*, 1988; Pearsall and Walde, 1994) and in western Canada (Roland, 1994; Roland and Embree, 1995). Meanwhile, Altenkirch (1991) reported a 30-year study of its population fluctuations in Germany. Tenow (1972, in Myers, 1988) reports studies in the Scandes Mountains from 1862–1968 showing irregular peak numbers, with a mean of 9.4 years. There have also been outbreaks on Sitka spruce (Hunter *et al.*, 1991) and on heather in Scotland (Kerslake and Hartley, 1997; Leggett *et al.*, 2011), the latter starting in 1980. Roland (1998) gives a commendably concise review.

Varley and Gradwell (1968) and Varley *et al.* (1973) made pioneering use of the biological properties of this insect to facilitate estimates of births and deaths for dynamical studies. In 1950 they selected five oak trees in Wytham Woods, Oxford, namely five patches (Section **12.2.1**), and continued annual censuses for 19 years. Twenty-five per cent of females emerging from pupae in the soil were trapped as they ascended trees to oviposit, a technique made possible because the brutes cannot fly. Dissection of these females allowed MPF to be estimated, while summer samples of descending mature larvae gave estimates of their survival and levels of parasitism from *Lypha dubia* (Tachinidae) (Section **10.2.5.7**). Parasitoids emerging from host's pupae were collected in inverted trays. The proportion of pupae attacked as larvae in the canopy by *Cyzenis albicans* (Tachinidae) and the ichneumon *Cratichneumon culex* were also estimated, that for the former being density dependent (Hassell, 1966). From this work, Varley developed the method of K-value analysis (Section **11.4.3**).

Phenology is peculiar. The moth emerges in November, December or even January, hence its common name. A few other moth species, however, also emerge during winter (Sattler, 1991). Male winter moths are fully alate and fly actively, if weakly. You may pick them up in car headlights on mild winter nights in country lanes. Their flight muscles operate at temperatures near 0°C (Heinrich, 1993). Even so, their ambit of distribution is restricted (Van Dongen *et al.*, 1997). Emerging females ascend forest and orchard trees. In southern UK, hungry titmice (Paridae) consumed them avidly (Betts, 1955). She estimated that they might eat ~20% of them, although these birds often eat seeds in winter. Once mated, females deposit ~150 eggs in small batches on the twigs, there being, of course, little possibility of their assessing the quality of larval food (Price, 1992; Section **10.2.4.7**).

Like lettuce root aphids on poplar (Section **3.3.3.1(a)**) and *Epirrita* on birch (Haukioja, 1980), an ecological problem for winter moths is a potential mismatch between bud burst and eclosion time, called *phenological asynchrony* (Watt and Woiwod 1999; Watt and McFarlane, 2002; Section **10.2.5.2**). If eggs hatch too early there is no food, if they hatch too late food is of increasingly poor quality. With oaks (*Quercus* spp.), the main food plants, some trees in a stand burst their buds far ahead of others, a spread of leafing times (Crawley and Akhteruzzaman, 1988). This may be a strategy by the trees to reduce caterpillar attack and so spread risk in time (Section **9.7**; Fig. 5.6). But when eggs are dense a greater *number* will likely hatch at the right time, since insect populations then spread in space and time (Andrewartha and Birch, 1954). Young leaves are tender and relatively protein rich, but low in tannins and toxins, making them preferred food (Feeny, 1970). But timing is difficult for the insect, since apart from the spread of bud bursting times, the physical environment affects plants and insects differently. Trees, in addition to any innate mechanism, respond mainly to rising soil temperature, while insect eggs, once their diapause is broken, respond to air temperature and insolation (Section **5.2.1.2(e)**). But there can be effective local synchrony between egg hatch and bud burst, achieved largely by the moth's local adaptation to the phenology of the trees: those with early leafing have moths that emerge and oviposit early (Van Dongen *et al.*, 1997).

Since females are flightless, both this local synchrony and the aerial dispersal by young larvae are

Fig. 5.6. Adjacent pedunculate oaks showing variation in the degree of bud burst.

understandable. Such larvae seek the periphery of the tree and secrete long silken threads until the breeze tugs them away. But although there is much movement even where food is plentiful (Holliday, 1977, 1985) greater dispersal is induced if the larvae cannot find food where they hatch (Wint, 1983), as when eclosion is mismatched to bud burst. While the polyphagous habit can be seen to be adaptive, the searching capability of individual larvae must be low. As in anemophily (Section **8.2.1.1**), it depends on diffusion, gravity and the vagaries of the wind, although leafy branches must 'strain' them out of the air. And while longer silken lines have greater lifting power (Bell *et al*., 2005), one expects them to be more readily entrapped. Having a variety of potential food types, *Prunus*, *Malus*, *Populus*, *Salix*, *Corylus*, *Crategus*, *Fagus*, and also recently Sitka spruce and heather, as well as *Quercus*, means that the resource target is much larger. But reproductive success is typically less on some of these alternative foods (Tikkanen and Niemela, 2000). Furthermore, larval ballooning apparently achieves population-wide redistribution. For example in the Orkneys, amplified fragment length polymorphism analysis (q.v) suggests few genetic differences *between* the several islands, indicating adequate panmixis (Leggett *et al*., 2011). Even so, genetic diversity *within* each island is high. The authors suggest that either the initial colonization from the mainland was *en masse* or has been a continuing process.

Polyphagy and springtime feeding are found in several outbreaking forest moths (Hunter, 1991). Then, dispersing larvae might well land on a tree in an unsuitable state. Temperature also influences survival. At 5°C, 50% of unfed *O. brumata* die in ~8 days, while at 20°C such mortality is expected in only ~2 days (Wint, 1983). We recall the high vulnerability of young juveniles in *Exophthalmus*, locusts and *Ostrinia*. With this moth and the lymantriid moths above, we have the rather infrequent case of food selection being largely a larval function (Section **10.2.4.7**): the adult female simply finds a tree near the place she emerged. The result in progeny distribution is comparable to, although the mechanism different from, the examples of *T. paludosa* (Section **3.2.1.2(f)**) and *C. fumiferana* (Section **5.2.1.4(c)**), and results in most progeny feeding close to the natal site and a remainder elsewhere, namely risk spreading in space.

Larval development normally takes ~6 weeks. Several parasitoids attack the larger caterpillars. In Europe, these include *Cratichneumon culex* (Ichneumonidae) and *Lypha dubia* and *Cyzenis albicans* (Tachinidae). These flies are attracted to volatile compounds produced when larvae munch leaves. Borneol from oak leaves is a specific attractant for *Cyzenis* (Roland *et al*., 1995). In the UK, great titmice, *Parus major*, feed large numbers of larvae to their chicks in early June (Betts, 1955). Insect eating at such times is also typical of normally granivorous birds (Polis and Strong, 1996). On oak, competition for food both intraspecifically and with the moth *Tortrix viridana* also leads to larval mortality (Hunter, 1998). In Norway, melanic larvae occur in response to crowding (Hagen *et al*., 2003). But while a significant reduction in pupal weight occurs at even moderate (~25%) levels of defoliation on oak and apple, larval survival is little affected (Roland and Myers, 1987). A further surprising finding of their work is that defoliation on a given tree in a current year may *increase* pupal weight and hence AF in the next year.

Within the soil several predatory beetles eat the pupae. *Philonthus decorus* (Staphylinidae), a major predator, acts density dependently (Varley and Gradwell, 1968). Pupae are in the soil in late summer and autumn, a time when temperatures are favourable for beetles to hunt. *Philonthus* shows numerical and aggregative responses (Roland, 1998; Section **10.2.3.9**). The carabid beetles *Feronia melanaria* and *F. madida*, whose adults range widely in European woodlands (Frank, 1967), may congregate to eat dense patches of winter moth pupae. But these beetles may stay to lay eggs, producing a numerical response. Other less important predators are *Abax paralle-lpipedus* (Carabidae) and *Quedius* and *Gyrohypnus* spp. (Staphylinidae). Beetles may destroy >90% of the pupae. Shrews (*Sorex*), wood mice (*Apodemus*) and voles (*Clethrionomys*) also eat them, probably in quantity, since all small mammals have high metabolic rates. When females emerge, normally during relatively mild weather, East (1974) found that 23% of them failed to reach the trees. Predatory birds such as *Turdus merula* and *Parus major* eat them on the ground, while *P. caeruleus* continues attrition on the trees (Betts, 1955), thus adding to their pre-reproductive mortality and reducing AF. In North America, the robin and blackbird are common predators (MacPhee *et al*., 1988). Adding to this complexity, the small mammals also eat the predatory beetles and the *Cyzenis* parasitoids in the moth's pupae.

There is evidence of cyclicity in winter moth populations, although it is not so strong as in, for example, *Choristoneura* and *Zeiraphera*. The cycles are ~10 years long, about the same duration as sunspot cycles (Section **2.2.2**), but this may be simple coincidence. Within Europe there is also evidence of synchronous cycles in different countries suggesting that regional weather may be driving them (Roland, 1998; Sections **11.3.1** and **11.5.2.3**). Unfortunately, studies seem not to have been done on the effect of harsh physical conditions on the moth's survival, which is surprising in view of the fact that they reproduce in winter.

In apple orchards in Nova Scotia, *Cyzenis* and *Agrypon flaveolatum* (Ichneumonidae) have been liberated for biocontrol. Winter moths are pests there only in mature orchards, possibly because the young, dispersing larvae have a higher success in locating trees in such situations (MacPhee *et al*., 1988). The moth seems to have been driven to extinction there by native and exotic enemies in many oak woodlands, and is declining in other parts of Canada.

In orchards, winter moth eggs were traditionally killed by winter washes (Section **13.3.3.2**). But the larvae often cause severe damage to the young leaves on untreated trees, and of course may 'balloon in' on their silken threads. Grease banding the trunks was another traditional method of defeating this pest: emerging females ascending the trees and ardent males searching for mates got stuck. This method might be used in the control of gypsy moths and *Melipotis*, a topical defoliator of the decorative tree poinciana, since the larger larvae move up and down between their feeding site in the canopy and diurnal refuges at the base of the tree.

There are several other notable pests of temperate forests. In the Geometridae, the univoltine North American canker moths *Alsophila pometaria* and *Paleacrita vernata* have some features similar to winter moths. Their flightless females deposit large egg masses in early or late winter, respectively. *Lambdina fiscellaria*, which has eastern and western sub-species, attacks hemlock, spruce and fir trees. *Epirrita* (= *Oporinia*) *autumnata* periodically defoliates Fennoscandian birch trees (Haukioja, 1980), while *Bupalus piniarius* is a European pest of pines. *Abraxas grossulariata* is a defoliator of gooseberry bushes. Species in *Agriopis*, *Chloroclysta* and *Erannis* are minor pests of fruit trees. In the Lymantriidae, *Euproctis chrysorrhoea* defoliates fruit trees, while *Orgyia pseudotsugata* damages Douglas firs and *Abies* spp. For *Orgyia*, trials using sprayable bead formulations of its sex pheromone have been made. In the Tortricidae, the North America *Acleris variana* (Miller, 1966) and *A. gloverana* are the eastern and western black-headed budmoths. Many European species (*A. comariana*, *A. cristana*, *A. laterana* and *A. lipsiana*) are minor pests of fruit tree, strawberry and *Rubus* leaves. *Archips*, with several species, is a related genus (Section **13.3.3.2**). In the Noctuidae, *Panolis flammea* attacks European pines and has outbreaked on *Pinus contorta* in northern Scotland (Hicks *et al*., 2001). Planting this pine in wet, acid areas allows a preferred species, Sitka spruce, to be grown later. The North American moth, *Hyphantria cunea* (Arctiidae) has spread from an original focus in Hungary into central and Western Europe (Alford, 2007). Its polymorphic (green/brown) larvae feed on forest and fruit trees, and can inhibit cyanogenesis when eating *Prunus serotina* (Fitzgerald, 2008).

Apart from *Choristoneura biennis* (above), several species of the northern European, noctuid genus *Xestia* have 2-year population cycles (Varkonyi *et al*., 2002). Because development takes 2 years, there are alternating annual cohorts, one dense, one sparse. Unlike *C. biennis*, in which the population cycles may be driven by weather (Zhang and Alfaro, 2003), *Xestia* cycles may be driven by an abundant ichneumonid parasitoid *Ophion luteus*. This parasitoid, with its *annual* life cycle, alternates between host cohorts possibly driving one to low density and the other to high density. This may be an unusual case of the overriding influence of a biotic factor in a physically harsh environment (Section **10.2.1**). But shrews eat *Xestia* pupae, which may also have an effect on these cycles.

5.2.1.4(h) LEPIDOPTERA; Pieridae. *Pieris brassicae*, the large white, *P. rapae*, the small white and *P. napi*, the green-veined white. Some other pierid genera. Often cosmopolitan pests of brassicas and some other crucifers. Several butterflies are habitat specific (Ford, 1946, 1975; Gilbert and Singer, 1975; Rainey, 1989; Cowley *et al*., 2001), and form metapopulations (Hanski *et al*., 1994; Hill *et al*., 1996; Section **12.3**). These include some *Pieris* spp. (Cappuccino and Kareiva, 1985; Ohsaki and Sato, 1994), but many *Pieris* and some related genera, such as *Ascia* and *Anteos*, are capable of steady, low-level migration (Baker, 1978; Jones *et al*., 1980). The *Pieris* spp. may be pests. In Europe, a generally northward migration, often on prevailing winds, occurs in early summer from the Mediterranean to cool temperate regions (Johnson, 1969). This is obvious in *P. brassicae*, where individual displacement of >400 km is recorded, although a majority of individuals die <300 km of their birthplace (Baker, 1978). There is evidence of a partial return migration in autumn (Spieth and Cordes, 2012). Large whites cannot overwinter in temperate Europe and the region is recolonized annually by vast numbers of them, with winter populations extending to India. Even the smaller *Pieris rapae* may extend its range by up to 170 km/year (Turchin, 1998). Migration of *Ascia monuste* in Florida often follows the coastline. Distances of up to 80 km at speeds of 10–15 km/h are recorded between areas of their widely spaced food plant, while direction and speed are largely independent of the prevailing winds (Nielsen, 1961). Asian species of *Hebomoia* are strong flyers (8–9 m/sec) and migratory. They feed on Cruciferae and Capparaceae. In Jamaica, several pierid butterflies, including *Ascia monuste*, *Phoebis sennae* and the big brimstone, *Anteos maerula*, show undistracted, unidirectional, low-level (2–3 m) migration from time to time (Freeman, unpublished data). Several other pierid butterflies have similar behaviour (Williams, 1958).

Pieris brassicae and *P. rapae* are not confined to distinct habitats, but fly from place to place and oviposit on any suitable food plant (Baker, 1978; Root and Kareiva, 1984; Ohsaki and Sato, 1990). Their migration and reproduction are not separate phases, as in most insects (Johnson, 1969; Section **10.2.4.1**). After mating, males douse their mates with benzyl cyanide, reducing subsequent mating and hence the chance of sperm competition (Fatouros *et al*., 2005). Several species of *Pieris* and *Colias eurytheme* show a post-mating, density-dependent emigration from their natal environment (Shapiro, 1970). But unlike many Pieridae, the wood white, *Leptidea sinapis* (South, 1906) and the rare *P. virginiensis* appear to be tenacious to a restricted habitat (Cappuccino and Kareiva, 1985).

By following a series of individuals that all had the same flight orientation, Baker (1978) concluded that each individual *P. rapae* has a unidirectional *life track* of several kilometres across the countryside, navigated by using the sun as a compass (Fig. 5.7). Average speed was only ~1 km/h as they tended to spend more time near food plants. Migration is not undistracted in Johnson's sense. Indeed, their low speed of passage may be a function of the mean distance between suitable food patches. In Baker's energetic work, mating and oviposition occurred during a 20-day displacement along the life track. Root and Kareiva (1984), while not quoting Baker's work, confirmed this linearity of flight path and reached the important conclusion that the offspring are more numerous on more scattered food plants. *Pieris rapae* females with a large egg load behave as if they are reluctant to leave a food plant, while those with

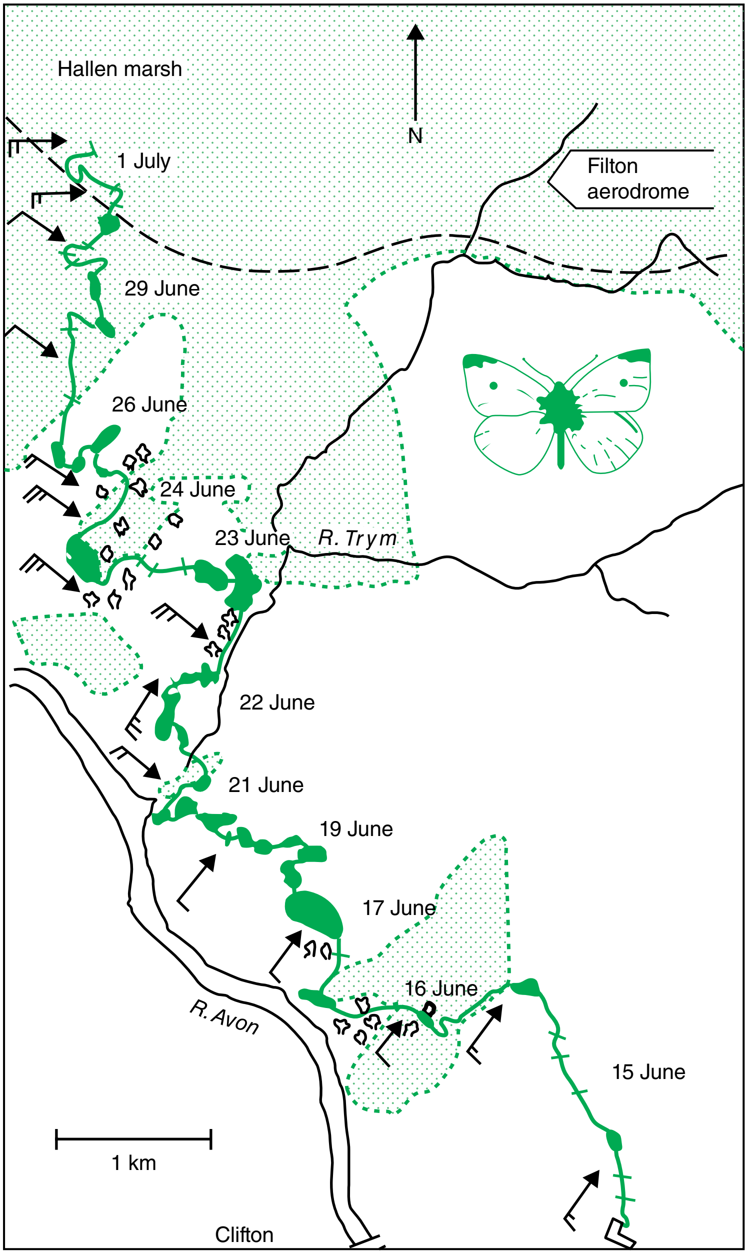

Fig. 5.7. The apparent life time flight path of a *Pieris rapae* butterfly across country. The path is derived from following a series of adults all flying in a similar direction. From Baker, R.R. (1984) *The dilemma: When and how to go or stay*. In: Vane-Wright, R.I. and Ackery, P.R. (eds) (1984) *The Biology of Butterflies*. Symposium of the Royal Entomological Society of London, No. 11. London, UK: Academic Press.

small loads are more vagile (Jones, 1977), but young plants are preferred to old ones. Myers (1985) found experimentally that at a distance, fertilized plants are greener and more attractive to *P. rapae*. While sinigrin is often thought to be the main attractant for these butterflies, the related glucobrassicin is more effective (Renwick and Chew, 1994). Food selection by *P. rapae* for their larvae also involves chemical deterrents of plant origin (Huang and Renwick, 1993). Also, oviposition deterring pheromones (Section **10.2.4.7**) are possibly applied during egg laying. This being said, Poelman *et al.* (2009) identified >400 compounds in the leaves of *Brassica oleracea*!

Eggs are deposited on sunny days, singly or in small groups, and cemented to brassica leaves. *Pieris rapae* prefers cabbage (*B. oleracea*) to other species such as radishes and kale, but red cabbages are seldom attacked. Early season populations may build up on cruciferous weeds. *Pieris brassicae* may feed on watercress. *Trichogramma brassicae* parasitizes newly laid eggs, being attracted by the benzyl cyanide donated by males. On Brussels sprout, *T. evanescens* homes in on synomones induced by *P. rapae's* eggs (Pashalidou *et al*., 2010, in Pérez *et al*., 2013). In *P. brassicae*, the young larvae are gregarious and the older ones solitary (Section **10.2.1**). *Cotesia* (=*Apanteles*) *glomerata*, a braconid wasp with gregarious larvae (Section **8.2.2.5(m)**), is the main parasitoid. In Japan, when *P. rapae* and *P. napi* are attacked together, *Cotesia* kills a higher proportion of the former because the larvae of the latter hide better and encapsulate the parasitoid larvae (Ohsaki and Sato, 1990). The interaction between these *Pieris* spp. might, without this careful work, be regarded erroneously as a case of resource competition (Sections **9.8** and **10.2.3.9**). *Pieris brassicae* reached Hokkaido, Japan, from Siberia, Russia, in 1996, colonizing the entire island and the north of Honshu, Japan, by 2000 (Tanaka *et al*., 2007). In Hokkaido, *C. glomerata*, which was formerly confined to *P. rapae*, rapidly evolved adjustments to this new host and increased its clutch size. Oddly, clutch size in *P. rapae* became reduced.

But in the USA, *P. rapae* larvae may encapsulate many of *C. glomerata's* eggs (Parker and Pinnell, 1973). Interestingly, larger sibling groups of *Cotesia* within a single caterpillar show higher survival, probably by more effective suppression of its host's defences (Ikawa and Okabe, 1985). *Cotesia rubecula* also parasitizes *P. brassicae*, but is a specialist on *P. rapae*. Both wasps are attracted to the complex plant volatiles that these brassicas emit when attacked (Takabayashi and Dicke, 1996; Poelman *et al*., 2009; Section **2.4.2**). *Epicampocera succincta* (Tachinidae) also parasitizes Japanese *Pieris*. European *Pieris* pupae are attacked by *Pteromalus puparum* (Pteromalidae) and by *Phryxe vulgaris*, a generalist tachinid parasitoid that infests both larvae and pupae of its numerous hosts (Colyer and Hammond, 1951). This wasp was introduced into New Zealand for biocontrol but unfortunately also attacks the endemic butterfly *Bassaris gonerilla*, which should have been foreseen. Birds and vespid wasps can be major predators of juvenile *Pieris* and cold weather in autumn curtails further development. In crops, an appropriate insecticide or microbial pesticides such as *Bt* or granulosis virus must be applied repeatedly to affect control. Strongly female-biased sex ratios in *P. rapae* are found in New Zealand (Creaser *et al*., 2008). Possibly this spanandry is due to local male-killing effects of *Wolbachia* (Section **10.2.3.9**), a bacterium occurring in many butterfly species.

Other *Pieris* spp. include *P. boeticus* in India, *P. candida* in South-East Asia and *P. melete* in Japan, where *P. napi* forms the sub-species *japonica*. In Japan, the last two species are relatively tenacious to their habitat, and lay fewer but larger eggs (Ohsaki and Sato, 1994). In the nineteenth century, the black-veined white, *Aporia crataegi*, could be a serious orchard pest in central Europe, but has now a much restricted range. In the USA, *Colias eurytheme*, the clouded yellow, attacks lucerne, clover and some other legumes. Again, there are multiple generations in the south and a northward migration in the early summer. In Jamaica by contrast, larvae of the yellow and white pierid *Kricogonia lyside* eat the foliage of lignum vitae, *Guaiacum officinale* (Zygophyllaceae), a wood used in carving. Periodically, masses of several hundred adults may be seen fluttering over the foliage of a tree and while the resulting larvae may affect considerable defoliation, they cause no obvious setback. Few other butterflies cause damage to trees, but *Papilio andraemon* and *P. demoleus* eat citrus in the Caribbean, and the nymphalid butterfly *Charaxes jasius* feeds on highbush blueberries in the south of Spain (Alford, 2007).

5.2.1.4(i) LEPIDOPTERA; Sphingidae.

Manduca (= *Protoparce*) *sexta*, *M. quinquemaculata*. Tobacco hawk moths. North American pests on solanaceous crops. These large (120 mm wingspan), powerfully flying moths can reach an air speed of ~50 km/h and in terms of resource seeking capability (ISC; Section **10.2.4.1**) are the apex of lepidopteran evolution. When female hawk moths are mature their ovaries pack the abdomen, but they lay eggs in ones and twos (South, 1920/1923; Kessler and Baldwin, 2001). The food plants are tobacco, tomatoes and potatoes and a few related weeds such as *Datura*. But despite the common name, tobacco is not a preferred food (Jermy *et al*., 1968). An adult may lay several hundred eggs distributed over >100 plants. Such a widespread egg distribution ensures that the entire progeny of a single female cannot, unlike those of *Lymantria* and *Malacosoma*

(Sections **5.2.1.4(e)** and **(f)**), die in a single disaster, an extreme example of spatial risk spreading (Section **9.7**). Indeed, most hawk moths space their eggs widely, although specific preferences and volatile organics emitted by attacked plants may well have influences (Kessler and Baldwin, 2001). They often eat vines (South, 1920/1923; Janzen, 1984). For example, *Agrius cingulatus* eats sweet potato, while *A. convolvuli* also feeds on these vines and convolvulus. While *M. sexta* larvae are essentially folivores, when large they may also eat the fruits.

But despite the wide distribution of progeny, hawk moth larvae often host parasitic wasps. *Manduca* eggs are parasitized by *Telenomus sphingis* (Scelionidae), while the gregarious *Apanteles congregatus* attacks its larvae. The latter is a generalist parasitoid, affecting several sphingid hosts, and so probably causing trans-specific mortality (Section **10.2.3.9**). In a further sequence, when *M. sexta* larvae feed on tobacco, the nicotine has adverse effects on this parasitoid. In experiments, more than half of them died and the survivors were smaller (Barbosa *et al*., 1991). The bugs *Jalysus spinosus* (the spined stilt bug) and *Geocoris pallens* suck the eggs and small larvae. Controls using either conventional insecticides or *Bt* must be done when the larvae are small, or the huge maturing larvae will do great damage to individual plants. Because the adults have energetic lifestyles they may be attracted to volatile chemical lures that mimic nectar sources and killed with an appropriate poison, such as 1% methomyl, as used for *Trichoplusia ni* (Landolt *et al*., 1991). We caution, however, that such a method would kill non-pest Lepidoptera.

5.2.1.4(j) LEPIDOPTERA; Noctuoidea, Noctuidae. *Spodoptera* (= *Laphygma*) spp., *Pseudaletia unipuncta*, *Mythimna separata*. Armyworms, or better, chenilles légionaires. Broad-spectrum pests of tropical to warm-temperate grassland and the crops adjacent to them. Basically, these are pests of grasslands, but like related cutworms, they attack a variety of plants *en passant*. Among several congeneric species, *Spodoptera exigua* and *S. exempta* eat rice, other cereals, cotton, beet, lucerne, tobacco, tomatoes and other crops. Their common names are derived from their habit of migrating, soldier like, in great masses of late larvae. Firstly, *S. exempta*, the African armyworm, has a phase polyphenism reminiscent of locusts (Rhoades, 1985). Larvae at low density are greenish, sluggish and develop slowly. Gregarious larvae are blackish, active and grow rapidly. The young adults too migrate *en masse*, and locally convergent winds ultimately result in concentrations of larvae (Pedgley *et al*., 1995). This species is found from sea level to 2500 m altitude. In the Nairobi, Kenya, region (~1500 m), complete development during outbreaks takes ~7 weeks, but at 32°C laboratory larvae mature in ~2 weeks. Larval densities >100/m^2 are common, while the areas they affect range from a few m^2 to tens of km^2. Such huge masses of insects overwhelm the predatory capacities of their enemies, a feature found in other massed insects such as locusts, cicadas and crane flies (Hamilton, 1971). Like locusts, they are capable of destroying a crop in a matter of hours. Odiyo (1979) in Kenya, estimated a mean density of final instar larvae as 28/m^2 covering an area of 65 km^2, their foliage consumption being ~50 tonnes/dw/day. In Nigeria in 1974, they devastated ~500,000 ha of rice and maize in a band 500 km wide across the country. A similar attack occurred in Sierra Leone in 1979.

In East Africa, Betts (1976) studied the migration of *S. exempta* around Lake Victoria. Severe attacks occurred in the Yemen in 1974, 1977, 1979 and 1984. The 1974 summer outbreak there was traced back to Zambia in November 1973, passing north through Tanzania, Kenya, Uganda and Ethiopia, and comprising over seven generations of migrants. Because of the long-distance adult migrations, these attacks were widespread and entirely unpredictable until tracking by radar was instituted. Infrared detectors can identify them by their specific wing-beat frequency (Rainey, 1989). These moths fly rapidly with the wind (~10 m/sec). This must be added to the wind speed as they do not settle periodically, like migrating locusts, nor maintain cohesive swarms. They often fly in a band 600–1100 m high with a ground speed of 30–35 m/sec (126 km/h; Section **10.2.4.5**). Atypically, laboratory evidence exists that migrant *S. exempta* have a higher reproductive output than the *solitaria* form (Rankin and Burchsted, 1992; Section **10.2.4**). Naturally, as in locust control, international co-operation and a pre-emptive strike policy are required if crop devastation is to be avoided. Originally both DDT and malathion were applied from the air. More recently, cypermethrin and other synthetic pyrethroids, which are >100 times more toxic to the larvae, have been used. Clearly, reduction in spray weight is critical in the economics of aerial spraying. At present there is interest in reducing the number of armyworms with viral preparations.

In California, *S. exigua* eats vegetable crops, such as tomatoes and celery. It also attacks groundnuts, preferring plants diseased with the fungus *Sclerotium rolfsii* on which its survival, size and presumably AF are enhanced (Cardoza *et al*., 2003, in Stout *et al*., 2006). *Spodoptera frugiperda* is found in South and Central America and in southeast USA, but adults often migrate as far as the Canadian border. In this adaptable species there are one to six generations annually according to prevailing temperatures, and evidence that strains adapted to maize and rice are undergoing speciation (Prowell *et al*., 2004). *Campoletis sonorensis* (Ichneumonidae) and *Cotesia marginiventris* (Braconidae) often parasitize the larvae. Despite this, their densities on maize in the southern states have been reported as 30,000–300,000/ha. Again, this pest attacks a wide variety of vegetables, cotton and lucerne. In Mexico, biocontrol using a variety of enemies has been promoted (Hoballah *et al*., 2004). *Spodoptera eridania* feeds on lima and other beans, being attracted to and tolerating the cyanogenic glycosides they contain. *Spodoptera littoralis* can be an important pest of highbush blueberries in the Mediterranean Basin. *Pseudaletia* attack cereals, on which the linear patterning of the larva is disruptive. As in other armyworms, cutworms and bollworms, the females are migratory, which, with their high AF (~1000), makes them formidable pests.

The oriental armyworm, *Mythimna separata*, is found from India through to northern Australia. In China, it migrates northwards from the southern provinces early in the year. Extensive mark/recapture work there, where >1800 pest forecasting stations exist, shows that individual moths are capable of flying up to 1400 km (Li Kwang-Po *et al*., 1964, in Rainey, 1989). Chen *et al*. (1995) have tracked massive spring migrations of this pest by radar. The moths may travel 200–300 km per night, and reach as far as Jilin province north of Korea. They move downwind in an altitudinal band of 200–400 m. But much of this migratory wave occurs more slowly, requiring three generations of the moth, tracking the northward advance of the growing season, laying eggs on wheat seedlings and causing extensive damage. In Korea, it is a regular pest every few years on cereals and grasses, and may even reach northern Japan. In China, a fourth generation develops on millet, maize and rice in the region 34–43°N, while a fifth generation attacks rice farther south. Although some southward re-migration occurs in early autumn it is on a much smaller scale than the spring mass movement, largely because the prevailing winds are less favourable.

Mythimna convecta is non-diapausing and tracks suitable food resources in eastern Australia. The main physical drivers are rainfall and lethal low temperature. Winter breeding occurs in the north (McDonald, 1995). In spring, grasslands and cereals are attacked progressively southward. Drying grasslands away from the coast further restrict this pest's distribution. High-level (1–2 km) migrations link the breeding areas. In North America, *Winthemia quadripustulata* (Tachinidae) parasitizes several armyworms, and may control *Pseudaletia* larvae locally (Davidson and Lyon, 1986). *Exorista japonica* attacks *M. separata* (Stireman *et al*., 2006). Other parasitoids are *Ophion bilineatus*, (Ichneumonidae) and *Chelonus insularis*, *Meterous laphygmae* and a few *Apanteles* spp. (Braconidae).

5.2.1.4(k) LEPIDOPTERA; Noctuidae. *Hyblaea puera* (now often placed in the Hyblaeidae). A pan-tropical defoliator of teak, some other hardwoods, and mangroves. This outbreaking moth (Beeson, 1941; Gray, 1972; Nair, 2007) is especially troublesome if rainfall is moderate, when it may reach larval densities of 15 million/ha, usually in discrete patches. In drought it may aestivate. AF averages ~500, the eggs being attached singly to veins on the underside of new leaves. Young larvae feed at the leaf margins and fold a little flap over themselves. Large larvae strip the huge teak leaves to the midrib and may cause total defoliation. Pupation is usually within a loose cocoon in litter, but under rainy conditions or in mangroves, within folded leaves. While most temperate outbreaking moths are univoltine, *H. peura* has 8–14 annual generations. It is not confined to teak. It also feeds on trees in the Bignoniaceae and Lamiaceae and defoliates mangroves. In India, outbreaks start when the pre-monsoon rains arrive and spread, wave-like, in successive generations (Nair, 2007). Initially, moths concentrate on hill tops, an example of the ultimate effect of topography in insect populations (Section **10.1.1**). Moths gradually move north with the advancing monsoons. Migrants are likely the source of these outbreaks, possibly originating in coastal mangroves. As in some other outbreaking moths, for example *Zeiraphera diniana* and *Spodoptera exempta*, melanic larvae predominate at such times. While in cool environments melanism is often associated with improved absorption of heat, in sunny ones it may protect from ultraviolet (UV) radiation (True, 2003).

Viral infections of *H. puera* are known, and it shares a number of parasitoids with another teak defoliator, *Eutectona machaeralis*, including *Eutachinus civiloides* and *Compsilura concinnata* (Tachinidae) and the wasps *Elasmus brevicornis* and *Eriborus gardneri*. Thus trans-specific parasitism (Section **10.2.3.9**) may exist, although *E. machaeralis* tends to occur later than *H. peura*. But control is difficult because of the moth's high fecundity and vagrant nature.

5.2.1.4(l) LEPIDOPTERA; Noctuidae. *Anticarsia gemmatalis*. Velvet bean caterpillar or soya bean looper. A broad-spectrum pest of legumes based in the Neotropics. This migrant moth maintains continuously breeding populations in the Neotropics and flies northward each spring through Mexico to affect the southern USA. The larvae defoliate leguminous crops including lucerne, velvet beans, soya beans and groundnuts. Entire fields may be stripped bare if migrants land there *en masse*. Thereafter, there are three or four generations before winter, which the moth rarely survives even in the Gulf States. The migration of this pest should be compared with those of *Pieris* and *Mythimna* above.

5.2.1.4(m) LEPIDOPTERA; Noctuidae. *Trichoplusia ni*. The cabbage looper. A polyphagous pest, mainly important in the New World, but also in Africa. Along with *Mamestra brassicae*, *Pieris rapae* and *Plutella xylostella*, this moth is a widespread pest of cabbages and other brassicas in North America. However, unlike them it also attacks several other crops in different families, including lettuce, lima and soya beans, cotton and citrus (Shorey *et al*., 1962). Near the Canadian border, its attacks are later in the year (July–August), having migrated from the south, and it can be difficult to control (Burkness and Hutchison, 2008; Caron and Myers, 2008). There are typically two annual generations, more in southern states. Development takes ~30 days at 27°C but ~90 days at 14°C. As in several swallowtail butterflies (Section **10.2.3.5**), there is an environmentally cued green/brown polymorphism of the pupae. Emergence occurs just before dusk. Unusually, males are a bit heavier than females, probably relating to the frequent multiple mating during which a large spermatophore is donated (Ward and Landolt, 1995). Both sexes are mutually attracted by pheromones. While fecundity is related to adult size, multiple mating increases it considerably: it may exceed 1000 in culture (Shorey, 1963) and 500 in the field; but longevity at ~15 days is unaffected. The eggs are usually laid singly, however, on the underside of the leaves on adjacent plants, females being attracted to mustard oils. *Voria ruralis* and *Compsilura concinnata* (Tachinidae) are parasitoids in parts of the moth's distribution. Integrated control can be achieved using reduced-risk insecticides such as *Btk* formulations or spinosad (Sections **13.2.3.2** and **13.3.2.4**). *Trichoplusia ni* is one of the few moths to have developed resistance to *Btk* (Caron and Myers, 2008). Conventional insecticides, such as lambda-cyhalothrin, may be less costly, but require more frequent application and result in a lower marketable yield.

The related *Pseudoplusia includens* can be a significant pest of soya beans. In Eurasia, another noctuid moth, *Mamestra brassicae*, is a Holarctic pest with a distinct fondness for brassicas, although like many noctuid moths it is broadly polyphagous, having been found on birch and oak. *Mamestra configurata* is a localized relative, being confined to parklands in western Canada, and may damage rape. Several species of *Orthosia* (*O. cruda*, *O. gracilis* and *O. incerta*) are occasional pests of apples and other fruit trees (Alford, 2007).

5.2.1.5(a) DIPTERA, NEMATOCERA; Cecidomyiidae. *Contarinia nasturtii*. Swede midge. An originally Palaearctic pest of brassicas, now an emerging pest in North America. This unusual pest is specific to brassicas, although they are variously susceptible (Hallett, 2007). Attack tends to be patchy. Northern Europe has two annual generations, Quebec, Canada, three to four (Corlay and Boivin, 2008) and France up to five. AF is ~80, eggs being laid in clusters on rapidly growing leaves and flower buds of several Cruciferae (Barnes, 1946). The larvae secrete saliva onto the plant tissue, which they digest extra-intestinally, causing deformation and scarring. In Europe, *Platygaster* and *Synopeas* (Proctotrupoidea) attack the late larvae. These wasps pupate in the host's larval skin and synchronize their life cycles with it, but are absent in Canada, where the midge is spreading rapidly (Corlay and Boivin, 2008). Mature larvae pupate in cocoons in the soil or enter winter diapause or summer quiescence according to conditions (Readshaw, 1966). Damage is most severe on broccoli, but the midge also forms reservoir populations on nasturtiums and some weeds such as *Capsella bursa-pastoris* (Hallett, 2007). Red cultivars show no enhanced resistance to this midge than white or green ones, suggesting that colour plays little part in food selection, as it may do in some other brassica pests. Rotation with a resistant crop should be practised and susceptible weeds removed. As in Colorado beetles, this is effective when a new susceptible crop is not too close to the old one. Some *Dasineura* spp. attack leaves, causing twisting, distortion and rolling up of the margins. *Dasineura mali* is on apples, *D. pyri* on pears, *D. tortrix* on plums, *D. tetensi* on black currants and *D. oleae* on olives. These midges are rather specific to their food plants. *Putoniella pruni* causes characteristic galls along the leaf midrib of plums.

5.2.2 Miners

Although ~10,000 leaf-mining species have been described (Connor and Taverner, 1997), relatively few of them are pests and most do little damage. Leaf mining became common in the Cretaceous (Scott *et al*., 1992) and is effectively confined to four major endopterygote orders, frequently in the Lepidoptera and Diptera, and less frequently in the Coleoptera and Hymenoptera (Hespenheide, 1991). Several families of small moths, including the Cosmopterygidae, Gelechiidae, Gracillariidae, Heliozelidae, Lyonetiidae, Nepticulidae, Tischeriidae and Tortricidae, commonly engage in leaf mining. Dipteran miners are largely in the Agromyzidae, but some drosophilid, ephydrid and muscid flies have a few. Coleopteran miners occur in the Buprestoidea, Cucujoidea, Chrysomeloidea and the Curculionoidea. *Promecotheca papuana*, the coconut leaf miner, is an offbeat chrysomelid miner. A few tenthredinid sawflies, such as *Metallus pumilus*, mine leaves when the larvae are small.

Unlike many munchers, the food plants of miners are usually quite specific (Hespenheide, 1991), possibly because of a more intimate physiological inter-relationship with them, and their feeding efficiencies are higher (Connor and Taverner, 1997). For example, some nepticulid miners induce the development of nutritious ‘green islands’ around themselves by producing a cytokinin (Engelbrecht *et al*., 1969, in Kahn and Cornell, 1983). Then mined leaves may be excised more or less frequently than healthy ones (Kahn and Cornell, 1983; Gripenberg and Roslin, 2008), so affecting the severity of attack. Mines are of two types: *serpentine mines*, in which single larvae snake their way through the leaf tissue, and *blotch mines*, in which several larvae live gregariously.

Miners suffer certain disadvantages compared with munchers, which arise largely from their confinement. First, their food is usually limited to a single leaf. Second, the mine compromises their mobility. Their cryptic habit does little to protect them. While they are less affected by pathogens they are often heavily attacked by parasitoids (Hawkins and Lawton, 1987; Connor and Taverner, 1997; Hawkins *et al*., 1997), less so by ichneumonoids, more by chalcidoids. Eulophid wasps frequently attack miners on British trees (Askew and Shaw, 1974). Birds, especially titmice, and ants (Hespenheide, 1991), also eat miners. In Jamaica, the ant *Crematogaster brevispinosa* commonly eats the larvae of *Liriomyza commelinae* in water grass, digging them out with one mandible (Freeman and Smith, 1990). Occasionally, coniferous needles are mined, as in the case of *Epinotia tedella* on spruce (Münster-Swendsen, 1991). In competition with munchers, miners are the likely losers. Munchers can crawl to another leaf, most miners cannot. The gelechiid miner *Tildenia*, however, may exit a leaf and enter another one (Price, 1992). Originating in South America another such miner, *Tuta absoluta*, has recently spread north and to Europe (Bawin *et al*., 2016). It affects tomato leaves but also mines the fruits and attacks plants in other Solanaceae, Malvaceae and Fabaceae. In *Recurvaria leucatella*, young larvae mine apple and pear leaves but overwinter in silken hibernaculae, attacking the leaves and flowers in spring. Miners are not dislodged by rain as exophytic larvae often are, but plants may excise mined leaves. Overall their survival to adulthood is greater than that of exophytic species, at ~10% as opposed to ~5% (Cornell and Hawkins, 1995). But the thinness of leaves physically restricts their size, so the adults are always small. Being the most important group, we will deal with the lepidopteran miners first.

5.2.2.1(a) LEPIDOPTERA; Tineoidea; Gracillariidae. *Leucoptera* spp. (sometimes placed in the Lyonetiidae). Chrysanthemum leaf miners. Narrow-spectrum pests of chrysanthemums and a few other Compositae. In temperate, decorative horticulture, exotic plants are often cultivated in heated glasshouses, although an increasing proportion of them are grown in warm countries and air freighted to the markets. Pests such as this one living in glass houses are ideally suited to be controlled biologically. The environment is contained; hygrothermal conditions often favour the parasitoid and to an extent can be manipulated by the grower. Such is the case here and with the whitefly *Trialeurodes* and its hymenopteran parasitoid *Encarsia* (Section **10.2.1**). Chrysanthemums have varieties whose beauty and diversity compare well with roses. They are expensive. No one wants a bunch of these flowers when the leaves are disfigured with mines. Certainly, it would look bad in a gift.

In parts of the USA, Eurasia south of 60°N, and in South Africa, another 'chrysanthemum leaf miner' is *Phytomyza syngenesiae* (= *P. atricornis* and *P. chrysanthemi*). But this beast is an agromyzid fly, warning us *not to rely on names in English*! *Leucoptera* spp. also attack lettuce and artichokes, typically resurging after spraying with parathion, as their eulophid parasitoids, especially *Chrysocharis ainsliei* and *Diglyphus* spp., are depressed (Lange *et al*., 1980). Alternative integrated pest management (IPM) methods (Section **13.3**) favouring these enemies are being developed. *Leucoptera malifoliella* and *Lyonetia clerkella* and *Ly. prunifoliella* mine the leaves of top fruits and may set back growth in saplings. *Phyllonorycter* is a speciose genus of leaf-mining moths, with *P. blancardella* on apples, *P. corylifoliella* and *P. cerasicolella* on other rosaceous trees, *P. coryli* on hazel and *P. messaniella* on oaks and some fruit trees.

5.2.2.1(b) LEPIDOPTERA; Tineoidea; Gracillariidae. *Perileucoptera coffeella*. Coffee leaf miner. A Neotropical, narrow-spectrum pest of coffee. The larvae of this small moth mine the leaves of coffee from Brazil to Mexico (Nestel *et al*., 1994) and the Caribbean. In Mexico, <8% of leaves were infected, but in Jamaica much higher levels than this have been common (personal data). Spraying coffee bushes against the borer *Hypothenemus hampei* (Section **6.3.1.1(b)**) with the highly persistent, chlorinated hydrocarbon endosulphan, which has been commonly practised here, kills the braconid and eulophid parasitoids that would destroy up to 60% of the juvenile stages of this miner. As a result this pest may spread unchecked, reducing large areas of coffee leaf so that the bushes appear brown. Because leaves are the plant's factories, the beans fail to mature, reducing both their quality and quantity.

Following this, a number of studies on the dynamics of leaf miners show that the main causes of juvenile mortality are parasitic Hymenoptera. For example, in *Liriomyza commelinae* such mortality is typically close to 95%, the majority due to the chalcid wasp *Chrysocharis majoriani* (Freeman and Smith, 1990). In California, the conservation of *Liriomyza's* parasitoids is a major consideration in the IPM of several vegetable crops (Trumble *et al*., 1997). In the UK, the nematode *Steinernema feltiae* shows promise to control *Liriomyza huidobrensis*, a pest of lettuce in glasshouses (Cuthbertson *et al*., 2007). In East African coffee, *Leucoptera meyricki* and *L. caffeina* typically outbreak from October to March (Bigger, 1973). While the giant looper on Kenyan coffee, *Ascotis selenaria reciprocaria*, consumes some miners, their numbers increase if parathion is sprayed. A battery of parasitoids including the braconid wasp *Apanteles bordagei* and the chalcidoid wasps *Cirrospilus variegatus*, *Achrysocharis ritchei*, *Elasmus leucopterae*, *Ageniaspis* spp. and *Pediobius coffeicola* attack them. A plethora of parasitoids, however, does not always depress host densities; often high host densities permit more parasitoids (Sections **5.2.1.4(d)** and **10.1**).

5.2.2.1(c) LEPIDOPTERA; Tineoidea; Gracillariidae. *Phyllocnistis citrella*. Citrus leaf miner. A potentially cosmopolitan pest of citrus. Some other gracillariid miners. Since 2000, this pest established itself in citrus orchards in Florida, USA, and then appeared for the first time on Jamaican citrus. It has characteristic clear, flat, serpentine mines. It also recently invaded Central America including Mexico, and Israel, Spain and South Africa. The pest originated in South-East Asia but spread to North Africa. It is thought that the little moths were transported from the latter area to Florida on the winds of Hurricane Andrew in August 1992. This is not a fanciful idea when one reflects on the regular ability of another small moth, *Plutella xylostella*, to migrate long distances (Section **5.2.1.4(a)**).

The small brown and silver moths are crepuscular or nocturnal and females lay ~50 eggs on new, pale-green citrus leaves (flushes). The larvae generally mine one side of the young, expanding leaf and pupate within it, usually at the edge. Development is rapid, generally under 2 weeks under favourable conditions, but as much as 7 weeks under unfavourable ones. Since a large proportion of the leaf area may be destroyed and many leaves attacked, this miner may reduce yield considerably. The confinement of *P. citrella* to the leaf during its entire development and the fact that the adults are short lived, is a weak link in the pest's biology, one providing a cultural strategy for control. Because they are confined to citrus, if flushes can be prevented for periods of several weeks, the miner populations can be reduced to low levels. This can be achieved by adjusting irrigation and fertilizer application. Where labour is cheap, such as in China and Thailand, hand picking of sporadic flushes can be effective.

In common with most leaf miners, this moth is attacked by several parasitoids. No less than 41 genera of chalcidoid parasitoids are recorded from it, including 33 eulophid and 4 pteromalid examples (Schauff *et al*., 1998). The parthenogenetic, encyrtid wasp *Ageniaspis citricola*, which originated in Thailand, shows the most promise for biocontrol. It has been used in Queensland citrus and exported to Florida. It is unusual in being host specific and also polyembryonic, producing up to eight adult females from each egg laid. Parasitoids originally present in Florida attack *A. citricola*, but have not been able to control it.

Another gracillariid miner, *Cameraria ohridella*, has recently become a widespread pest of European horse chestnut trees. While a large proportion of the leaves are attacked, particularly at lower levels in the tree, and several annual generations occur, lasting damage is not yet apparent, possibly because the bulk of their activity takes place later in the year after the leaves have passed peak production. Some species of *Cameraria* are associated with oaks in California. The many species of *Phyllonorycter* are leaf miners, including *P. crataegella* on apples and several species on oaks. Recently, two other congeneric moths, *P. leucographa* and *P. platani* have colonized south-east England.

5.2.2.1(d) LEPIDOPTERA; Tineoidea, Heliozelidae. *Coptodisca splendoriferella*. The resplendent shield bearer. An occasional pest of top fruits in North America. This very pretty little moth has extraordinary habits. Adults are silver and gold with chocolate streaks on the wings. The young larvae mine the leaves of top fruits and their wild relatives in the Rosaceae. The mine is at first linear but later is enlarged to become a blotch. Mature larvae leave the confines of the mine and make a case lined with silk, using the leaf cells, and attach this to a branch. Blotch mines become necrotic and finally give the leaf a perforated appearance. Diapausing larvae pass the winter in these cases, so avoiding the consequences of leaf fall. They pupate in spring and, emerging shortly afterwards, oviposit on the unfolding leaves. In addition, there may be a summer generation. *Coptodisca negligens* has recently become a significant pest of cranberries in parts of the USA. The moths overwinter as eggs and the young larvae attack the new foliage in spring.

The Nepticulidae contains a fair number of species in the genus *Stigmella*. These include *S. aurella* on blackberries, *S. fragariella* on raspberries, *S. pomella* and *S. malella* on apples and *S. pyri* on pears and plums. They tend to be very specific but their damage usually minor. The heliozelid miner *Antispila rivillei* can damage the leaves of grapevines significantly.

5.2.2.2(a) DIPTERA; CYCLORRHAPHA; Muscidae. *Pegomyia betae*. Beet leaf miner. A temperate pest of seedling beet. Like flea beetles, these are essentially agricultural pests of seedling sugar beet and mangolds and have some similar ecological properties to them regarding damage, especially in relation to temperature and moisture. Females can lay several eggs on larger seedlings and the larvae mine the leaves, reducing their photosynthetic area. Some beet cultivars with smooth leaves, such as AJ3 and AJ4, are less attractive to them (Zhang *et al*., 2008). Plants with 4–8 leaves can normally resist the attack, but their development will be set back according to its intensity and dryness of the soil. In North America *P. hyoscyami* has recently become important on seedling sugar beet, largely due to precision seed drilling. It also attacks spinach and chard, sometimes making these leaf crops unsaleable in that fastidious market in which appearance is everything. Deep ploughing will kill some of the overwintering puparia. A few species of agromyzid flies occasionally affect fruit and vegetable crops. They include *Agromyza flaviceps* and *A. igniceps* on hops, *A. potentillae* on raspberry and strawberry leaves and *Phytomyza heringiana* on apple leaves.

5.3 Sucking Pests

5.3.1 General introduction

Although many such insects have a preference for feeding on the apices of soft stems, we will consider them as feeders on apical foliage; indeed, several are not confined to this region of the plant. They are exclusively hemipteroid exopterygotes (Gündüz and Douglas, 2009), with nymphs and adults often living side by side in a similar fashion (see **Chapter 6** for thrips). This group feeds characteristically on ruderal plants (Brown, 1985), at least in temperate regions. So we expect them to be adapted to field conditions and to attack the cultivated relatives of these plants, namely vegetable and grain crops. With the exceptions of the fruit-piercing moths *Gonodonta* and *Alabama argillacea*, adult *endopterygotes* with sucking mouthparts do not attack plants, although of course they frequently imbibe nectar.

Although several heteropteran bugs in the Coreidae, Lygaeidae, Miridae, Pentatomidae and Pyrrhocoridae are major plant pests, in the main the phytophagous homopteroids take centre stage here. The aphids are the most important group, but other notable pests occur in the Cicadellidae, Fulgoroidea, Psylloidea, Aleyrodoidea and Coccoidea. These groups show increasing association with their plant food, but in the main a reduction in adult body size. Many homopteroids can spread plant viruses and occasionally bacteria, while cicadellid, delphacid and psyllid bugs are the main culprits in the transmission of phytoplasmas (Lee *et al*., 2000; Weintraub and Beanland, 2006). None of the xylem-feeding cicadid, cicadellid or cercopid bugs have been shown to transmit viruses. As we have seen, their efficiency as transmitters depends on their degree of mobility between plants. As in the spread of mammalian diseases (Section **7.1.1.4**), a vector must pick up the pathogen in an individual victim and move with it to another. But for viruses it also depends on whether the virions exist briefly in the insect's mouthparts or foregut, or are persistent and circulate within it. Virions may also multiply within the vector, and may pass to the next generation via the egg (Ossiannilsson, 1966; Nault, 1997). Again, a persistent virus can affect the survival of the vector. With phytoplasmas, which are degenerate Gram-positive prokaryotes related to mycoplasmas and spiroplasmas, and formerly called mycoplasma-like organisms, there is evidence that the pathogen may sometimes *increase* the reproductive success (RS) of its vector. Phytoplasmas are essentially bacteria lacking cell walls, limited to the sieve plates of the phloem, and so only insects feeding there can transmit them (Lee *et al*., 2000). Many more diseases are known than there are known vectors: they include stunt, yellows, yellow dwarf and witches broom diseases of several crops. Then aphidoid and coccoid bugs, in particular, are often more successful when their food plants are stressed for water (White, T.R.C., 1978), because amino acids are less dilute. Indeed, waste plant sap is deposited as honeydew beneath the feeding colony. These deposits attract specific fungi, but also the many hymenopteran parasitoids. Some Heteroptera, too, transmit phytopathogenic organisms, but are particularly associated with *Phytomonas* (Dollet, 1984; Camargo, 1999) and fungi (Mitchell, 2004).

5.3.1.1(a) HETEROPTERA; Lygaeidae. *Blissus leucopterus* and *B. insularis*. Chinch bugs. New World pests of cereals and grasses. Some additional lygaeid pests. The former black and white bug moved up from South America in the 1700s where it fed on maize and wild grasses. It now reaches Canada, but does most harm in the Mississippi watershed, where it outbreaks periodically. It damages grain crops including maize and sorghum, but also greensward. In some areas there are short- and long-winged forms (Borror *et al*., 1989). There are two generations per year in the north and three or more in the south, while the closely related southern chinch bug, *B. insularis*, may have up to seven generations in southern Florida.

Blissus leucopterus lays several hundred pale yellow eggs at a rate of 15–20/day. The nymphs are at first red, but gradually acquire adult coloration through five instars. The first generation often attacks green, succulent wheat and barley. The new adults appear in June and are more important on maize and sorghum, onto which they migrate. Second-generation adults, the overwintering stage, appear in September. The most preferred site for hibernation is deep turf along roadsides, hedges and fences. This bug thrives in hot, dry weather and so prefers thinly spaced crops with low humidity. Heavy rain drives the eggs and young nymphs into the mud and persistent high humidity encourages the spread of the common green muscardine fungus, *Beauveria bassiana*. *Orius tristicolor* (Anthocoridae), *Geocoris* spp. (Lygaeidae) and a variety of birds are significant predators. *Eumicrosoma beneficum* is a scelionid parasitoid of the eggs. A switch to legumes, which are totally resistant, may be necessary if chinch bugs cause persistent trouble, although some maize varieties are resistant. Damage is often greatest where maize is planted near wheat or barley, but insecticidal barriers between these crops can stem the problem.

Several species of *Lygus* are pests, including *L. hesperus* on strawberries, *L. pratensis* on potatoes in Russia, and *L. lineolaris* on lucerne, tomatoes, strawberries, peaches and cotton in the USA. The last, called the tarnished plant bug, has become troublesome in the mid-southern cotton belt on flowering cotton, because the widespread adoption of transgenic *Bt* cultivars against boll weevils has led to a reduction in spraying (Musser *et al*., 2007). It is parasitized by *Leiophron pallipes* (Braconidae). The polyphagous *Ly*. *rugulipennis* attacks lettuces in Sweden and pine seedlings in Finland, but may be lured onto a trap crop of the weed *Senicio vulgaris* (Hokkanen, 1991). It also transmits Potato Mosaic Virus M (Turka, 1978, in Mitchell, 2004). Other *Lygus* spp. vector *Erwinia amylovora* to pear fruits, a bacterial genus also transmitted by *Anastrepha* fruit flies (Section **6.3.1.1(n)**). All *Lygus* spp. must be suspects for transmitting phytopathogens. Apart from conventional spraying, control of many of these bugs has been tried with trap crops (Shelton and Badenes-Perez, 2006).

5.3.1.1(b) HETEROPTERA; Miridae, Pentatomidae, Piesmidae, Coreidae, Tingidae. A diversity of these bugs attacks crops, although few of them could be regarded as major foliar pests. *Capsus cinctus*, *Labops* and *Irbisia* spp. feed on rangeland grasses in North America. Another mirid bug, *Neurocolpus nubilus*, occurs on mid-southern cotton in the USA. The Piesmidae are a small family feeding mainly on the Chenopodiaceae (Richards and Davies, 1988). *Piesma quadrata* and *P. cinereum* spread some viruses affecting sugar beet in Central Europe and North America, respectively. The virus replicates and overwinters in *P. quadrata*, which hibernates in crevasses in the bark of trees and other sheltered places. Interestingly, two congeneric bugs, *P. maculatum* and *P. capitatum*, are not vectors (Ossiannilsson, 1966). *Stephanitis pyri* (Tingidae) attacks many trees in the Rosaceae, especially apples, pears, plums and cherries, tending to be most serious in continental Europe. Adults oviposit along the midrib of the leaf, which may become clorotic with later feeding by all stages. Their faeces block the stomata and sooty moulds then develop (Alford, 2007). There are two to three annual generations, and adults pass the winter under leaves and bark. Many other Heteroptera transmit plant diseases (Mitchell, 2004; Section **6.3.2.1(a)**). *Anasa tristis* (Coreidae) is widely distributed in the Americas and attacks a variety of cucurbits voraciously (Fargo *et al*., 1988). These squash bugs inject a toxin causing leaf necrosis and transmit cucurbit wilt disease. They may also attack the fruits. In several states they transmit the phloem-limited bacterium *Serratia marcescens*, the agent of lethal cucurbit yellow vine disease. They overwinter in sheltered situations and can transmit this bacterium in the following year (Pair *et al*., 2004). The bugs are multivoltine in warmer regions, and control early in the year is essential if dense populations are to be avoided. Two other coreid bugs, *Clavigralla tomentosicollis* and *C. shadabi*, attack cowpeas.

5.3.1.2 Homopteroids

5.3.1.2(a) AUCHENORRHYNCHA; Cicadoidea, Cicadellidae. >25,000 spp. *Empoasca fabae* s.l. Polyphagous 'potato' leaf hoppers. Other cicadellid pests, vectors of diverse pathogens but particularly phytoplasmas. A distinguishing behaviour of cicadellid bugs is their habit of scuttling sideways when prodded. More intimately, many of them have been found to contain the endosymbiotic bacterium *Baumannia cicadellinicola*, which enhances their nutrition, as they often imbibe xylem sap (Baumann, 2005). The Typhlocybinae, however, suck out the sap from leaf mesophyl cells (Strong *et al*., 1984). The group is important in transmitting plant viruses, phytoplasmas (Lee *et al*., 2000) and related organisms, with migrants moving through diverse spatial scales.

Empoasca fabae s.l. was originally regarded as a single species, but is now divided into four sibling species: *E. fabae* s.s., *E. filamenta*, *E. abrupta* and *E. arida*. *Empoasca fabae* s.s. is found mainly in eastern North America, often migrating rapidly up the so-called Mississippi Flyway in spring from narrow areas close to the Gulf Coast where it overwinters. Migration occurs on warm, southerly winds at 600–1600 m altitude (Johnson, 1995). Less spectacular, iterative return migrations occur in autumn (Taylor and Reling, 1986b; Johnson, 1995), when the passage of cold fronts moving to the east stimulate exodus flights and southward air flows occur. *Empoasca filamenta* is found in arid, high altitude regions of the Rocky Mountains, while the other two species inhabit the Pacific Coast.

Empoasca fabae has several generations per year according to temperature, with a minimum generation length of 3–4 weeks. Each female inserts 50–100 eggs into the stems and large leaf veins of crop plants such as potato, lucerne and soya beans. Feeding from the phloem causes blockage of these vessels, resulting in apical chlorosis. *Empoasca devastans* causes similar damage to potatoes in India, while *E. fascialis* and *E. lybica* are African cotton pests that attack this and other crops such as cassava, castor and groundnuts. *Cicadulina* spp. transmit Maize Streak Virus there. *Empoasca mali* and *Typhlocyba pomaria* are pests of apple foliage. The polyphagous *Circulifer tenellus* is a specific vector of Beet Curly Top Virus in the USA. Both bug and virus have huge populations on desert weeds, mainly Cruciferae and Chenopodiaceae, whose presence is the result of sporadic farming and overgrazing. *Circulifer tenellus* also transmits *Spiroplasma tenella* (= *citri*), which causes stubborn disease of citrus (Lange, 1987).

The six-spotted leaf hopper, *Macrosteles fascifrons* s.l., has similar migratory behaviour to *E. fabae* s.s. It continues to breed in the southern states, and migrates in May as far north as the Canadian border (Johnson, 1969). The bugs overwinter as eggs in the soil but are augmented each spring by a new wave of largely female immigrants. This species attacks a range of crop and decorative plants, and transmits Aster Yellows. *Macrosteles quadripunctulatus*, among some other cicadellid bugs, transmits Chrysanthemum Yellows (CY) phytoplasma from infected to uninfected chrysanthemums. CY also infects periwinkle and celery, but the bug cannot acquire this phytoplasma from the latter crop plant, which is thus an example of a *dead-end host* (Weintraub and Beanland, 2006). While *Oncopsis alni* breeds only on *Alnus* it is a secondary pest of grapes, transmitting Grapevine Yellows (Alford, 2007).

Similar pests include *Nephotettix virescens*, *N. nigropictus* (= *apicalis*) and *N. cincticeps* (green rice leaf hoppers), which often have alternative food plants in diverse grasses, and vector several viruses such as Tungro Virus, Yellow Dwarf, Transitory Yellowing (Hill, 1983) and Waika Viruses (Kisimoto, 1984), and some phytoplasmas. Two other cicadellid pests of rice are *Recilia dorsalis* and *Thaia oryzivola*, the former transmitting Dwarf and Orange-leaf Viruses. In the Holarctic, *Psammotettix alienus* is a grassland and cereal species that specifically transmits Wheat Dwarf Virus in winter wheat (Lindblad and Areno, 2002). As in the case of attack by *Opomyza*, late sowing avoids transmission of the virus, especially in mild autumns.

Dalbulus maidis is a grass-feeding cicadellid bug whose distribution extends from Argentina to southern USA. It transmits three pathogens of maize: maize stunt spiroplasma (*Spiroplasma kunkelii*), maize bushy stunt spiroplasma and Maize Rayado Fino Marafavirus, the first-named being the most important as it occurs throughout the region. Extensive areas of this crop are grown in the rainy season (May–October) in Mexico at elevations >1000 m, but during the dry season provide no suitable habitat for *D. maidis*. These workers show that this bug persists in the wet lowlands during the November–April period only to migrate to upland regions later on, carrying these pathogens with it. Huth (2000) reviews the viruses affecting cereals and grasses.

Homalodisca coagulata is a polyphagous leafhopper that may be important in vineyards since it transmits the bacterium, *Xylella fastidiosa*, causing Pierce's disease (Redak *et al*., 2004). *Homalodisca vitripennis* has recently become a pest in California where citrus and grapes are grown adjacently. While preferring citrus, it easily spreads into vineyards. Changes in the IPM of citrus, with a reduced use of broad-spectrum insecticides, may have allowed this bug to outbreak. Other cicadellid vectors include *Draeculacephala minerva* and *Carneocephala fulgida*, which are major vectors in the Central Valley, and *Graphocephala atropunctata*, which is more important near the coast (Purcell and Frazier, 1985). The latter species is common along the edges of streams, while *C. fulgida*, now often called *Xylophon fulgida*, is associated with irrigated pastures (Sisterson *et al*., 2008). Some of these vectors build up their populations in damp situations on grasses, sedges and rushes and are more numerous in wet years.

Several *Erythroneura*, including *E. elegantula* and *E. variabilis*, attack grape leaves in California. The parasitoid of their eggs, *Anagrus epos* (Mymaridae), is more successful in the former species, driving its numbers down differentially. This is a similar dynamic to that of *Apanteles glomeratus* (Braconidae) on mixed populations of *Pieris* species in Japan (Ohsaki and Sato, 1990; Section **5.2.1.4(k)**) and of *Melittobia* on primary wasp species and the inquilines that reuse their cells in Jamaica (Freeman, 1977; Jayasingh and Freeman, 1980; Section **10.2.3.9**). Of course, two or more parasitoid species often attack a single host (Varley, 1941, 1947; Morris, 1963; Huffaker and Kennett, 1966; Freeman and Geoghagen, 1989; Turchin, 2003), which reminds us that relationships between a guild of parasitoids and their several shared hosts will be complex (Askew and Shaw, 1986; Bonsall and Hassell, 1997, 1998; Godfray and Muller, 1998). The system is also complicated because *Anagrus* requires an alternative winter host (Doutt and Nakata, 1973). *Erythroneura elegantula* passes this period as reproductively diapausing adults. But another cicadellid bug, *Dikrella cruentata*, provides this seasonal bridge as it breeds throughout the year. However, its food plants are the *Rubus* spp. that often grow abundantly along the banks of streams. So in spring and summer this wasp spreads into the vineyards from a continuing *Anagrus/Dikrella* system along the streams. These authors show that, despite its minute size (Section **8.2.2.5(o)**), *Anagrus* penetrates the vineyards by several kilometres.

Scaphoideus titanus is the specific cicadellid vector of a phytoplasmal disease of grapevines in Europe, called *Flavescence dorée* (Bressan *et al.*, 2006). This bug is univoltine and confined to vines. In North Carolina, USA, *Scaphytopius magdalensis* transmits stunt disease of blueberries. *Myndus crudus* is a vector in Florida, USA, of the phytoplasma causing lethal yellowing of coconuts, while in Jamaica a species of *Cedusa* is apparently the culprit (Brown *et al.*, 2006). Although their sample size was small (43 bugs), a high proportion (30%) were found to carry this phytoplasma. *Macropsis mendax* similarly transmits elm yellows phytoplasma (Weintraub and Beanland, 2006).

5.3.1.2(b) STERNORRHYNCHA; Psylloidea; Psyllidae. Many of these insects, which are known from the Jurassic (Scott *et al.*, 1992), build up dense local populations on woody dicotyledons, often outstripping the depredations of their enemies. They may operate outside their *release point* (Southwood and Comins, 1976; Section **11.2.2.5**), inverse density dependence ensuing. In Northern Europe, sallow (*Salix caprea*) trees are frequently checked by large populations of psyllid bugs (Fig. 5.8). Australasia has a rich psyllid fauna with many species living on Eucalyptus (Clark and Dallwitz, 1975). In Jamaica, one often sees yellowing of *Samanea saman* trees by a psyllid bug, possibly *Heteropsylla cubana*. Although most of the ~2500 described species suck leaves and their petioles, some form galls on apical shoots. Psyllid bugs feed principally on phloem sap and employ the endosymbiotic bacterium *Carsonella rudii* to augment their nutrition.

In its native region of the Caribbean and Central America, *H. cubana* attacks the terminal shoots of *Leucaena*, but is not a major pest. This fast-growing leguminous tree is used for cattle fodder, green manure and fuel. But the bug has spread westward since the 1980s to South-East Asia, India and East Africa (Nair, 2007). In such exotic situations (Indonesia, the Philippines, parts of Thailand), there were initial outbreaks in *Leucaena* plantations. In Kenya, such outbreaks were associated with regrowth foliage that occurred after the rainy season (Ogol and Spence, 1997). More recently its populations have declined. This may be a result of increasing adaptation of parasitoids (*Tamarixia lucaenae* and *Phyllaephagus* spp.), and of generalist predators, but also by several fungal pathogens, (*Entomophthora* and *Fusarium* spp., *Conidiobolus coronatus* and *Neozygites heteropsyllae*) that, as usual, are especially virulent in high humidity. In West Africa, *Phytolyma fusca* and *P. lata* gall the important hardwood trees *Milicia excelsa* and *M. regia* (iroko), respectively. The nymphs live in galls along the midrib, development taking ~3 weeks (Wagner *et al.*, 1991). When the galls rupture, releasing the adult, the leaf tissue often becomes infected by saprophytic fungi, causing dieback. In Ghana, plantations of iroko have been frequently unsuccessful.

Fig. 5.8. Sallow trees attacked by psyllid bugs, probably a species of *Cacopsylla*, in Ireland.

The psyllid bugs *Cacopsylla mali* and *C. pyricola* are, respectively, the apple and pear suckers, the latter being a key pest in France and some other European countries. The encyrtid wasp, *Trechynites psyllae*, is its major parasitoid (Sullivan and Völkl, 1999). While originally European, these bugs are now found in North America and other places where pome fruits are grown. They are rarely significant orchard pests, although *C. pyricola* vectors Pear Decline Virus and some phytoplasmas (Weintraub and Beanland, 2006) and can be damaging in western North America. The honeydew from their feeding encourages the growth of sooty moulds, which of course compromise photosynthesis.

In citrus orchards *Diaphorina citri* damages young plants and builds up numbers rapidly on new flushes, AF often being >1000. It transmits *lethal greening* *disease* or *huanglongbing*, caused by the phytoplasma *Candidatus* infesting the phloem. This nasty combination, long known in India, is widespread in China, extending to 29°N over the last century (Yang *et al.*, 2006). Although the bug migrates northward in summer, mountain ranges restrict its movement (Section **10.2.4.5**). It recently reached Brazil (Halbert and Manjunath, 2004), and also Florida and Texas in the USA. It feeds on several trees in the Rutaceae, forming a reservoir population. Citrus fruits become discoloured and taste bad. Grafting can spread the disease and insecticidal control is ineffective. Cures are yet to be developed, although applications of β-aminobutyric acid may well improve plant resistance to the vector (Tiwari *et al.*, 2013; Section **2.4.2**). Seven other *Diaphorina* spp. are recorded from citrus. *Trioza erytreae* transmits a variant of this disease in South Africa.

In field crops, *Paratrioza cockerelli*, attacks the foliage of potatoes and other solanaceous plants in the USA from New Mexico to Nebraska, migrating northwards as the summer approaches. They cause yellowing and loss of production. *Paurocephala gossypii* occurs on cotton in parts of tropical Africa and, like *C. pyricola*, may transmit a disease (psyllose) of that crop plant. *Bactericera trigonica* transmits stolbur phytoplasma to carrots.

5.3.1.2(c) STERNORRHYNCHA; Aleyrodoidea, Aleyrodidae (~1500 spp.) (= Aleurodidae). *Bemisia tabaci* s.l. Sweet potato, cotton or tobacco whiteflies. Sub-tropical and tropical pests and virus vectors, affecting several dicotyledonous crops. Several other whiteflies. Whiteflies are haplodiploid (Normark, 2003). They show a further close association with their plant food, for only crawling first instar nymphs and the adults have any mobility. Reciprocally, the leaf structure, and chemical profiles induced by their presence, both defensive and nutritional, determine their RS (Inbar and Gerling, 2008). Indeed, many of their relationships with the biotic environment are mediated through food plants. Whiteflies contain the endosymbiotic bacterium *Portiera aleyrodidarum*, providing them with essential nutrients (Baumann, 2005). Other such symbionts include *Rickettsia*, *Cardinium*, *Hamiltonella*, *Arsenophonus* and *Wolbachia*. Interactions often exist between whiteflies and other species feeding on the same plant. For example, leaf miners are commonly adversely affected by whiteflies. Conversely, *Heliothis* larvae feeding on cotton fruits may improve the quality of leaves for whiteflies.

The *Bemisia tabaci* complex attacks tobacco, tomatoes, cotton, grapes, cassava, brassicas, and several other crops. The taxon represents several cryptic species (Perring, 2001; Inbar and Gerling, 2008) that are often described as 'biotypes' (Walter, 2003). Biotypes B and Q have become very invasive recently (Xu *et al.*, 2010). Indeed, 11 'well-defined genetic biotypes' are now recognized (Cuthbertson, 2015). They are minute (~1 mm) and resemble the greenhouse whitefly, *Trialeurodes vaporariorum*, but have greenish-yellow bodies and white wings, the latter species being all white. They reproduce sexually and the females, who have an AF of up to 300, lay characteristic semi-circular egg clusters. Each egg has an appendage inserted in a plant stoma. Stage 2–4 nymphs are ovoid, scale-like and lack much mobility. But rather like psyllids, the adults make little flights away from, and back to, the plant if it is shaken. Populations build up on individual plants and, depending on conditions, the life cycle takes 2–3 weeks.

Aphelinid wasps (*Encarsia lutea*, *En. pergandiella*, *En. sophia*, *En. formosa*, *En. transverna*, *Eretmocerus mundus* and *Er. melanoscutus*) are parasitoids of this complex. They also kill the whiteflies by feeding on them (Zang and Liu, 2008). Coccinellid beetles are general predators, while the thrip *Aleurodothrips fasciapennis* is a more specialized predator, also feeding on *Dialeurodes citri* in Florida (Comstock, 1940). Studies in glasshouses (Cuthbertson *et al.*, 2007) show that the entomopathogenic nematode *Steinernema feltiae* provides effective control, while fungi and predatory mites are also useful.

The insect itself is particularly damaging during drought, resulting in chlorotic leaves and stunting. Like aphids it secretes sticky honeydew. Even so, hot dry winds in Israel suppress outbreaks, while rainstorms can be a major mortality factor during development (Asiimwe *et al.*, 2006). These bugs spread many plant viruses (Brown and Czosnek, 2002; Asiimwe *et al.*, 2006), including Tobacco, Tomato and Cotton Leaf Curl Viruses, Cassava Mosaic Virus, Lettuce Infectious Yellows, and Virus B of sweet potatoes, the biotypes transmitting viruses selectively. *Bemisia tabaci* has two forms of flight behaviour (Isaacs and Byrne, 1998): a majority flies low down seeking fresh food, but a minority has an upward migratory flight. It is known to redistribute up to 2.7 km and has been trapped at >300 m in the air, suggesting that it can move much further. *Bemisia argentifolii* has been separated from this complex fairly recently. It is a cosmopolitan broad-spectrum pest attacking diverse crops (Solanaceae, Leguminosae, Cruciferae) in glasshouses and fields, being especially important on Californian cotton. It also forms reservoir populations (Section **13.1.2.2**) on some weeds, and has many parasitoids in common with *B. tabaci*.

Dialeurodes citri occurs in parts of Asia and the Americas on citrus and coffee, while *Aleurothrixus floccosus*, the woolly whitefly, also afflicts citrus and figs (Alford, 2007). *Trialeurodes floridensis* damages avocados, *T. vittata* grapes and *T. packardi* strawberries. In Latin America, *Aleurotrachelus socialis* attacks cassava. *Siphonus phillyreae* is common in the Eastern Mediterranean. Hassell *et al.* (1987) made a long-term population study in the UK on the viburnum whitefly, *A. jelinekii*, from 1962 until the 1980s. Their studies show that adults are reluctant to leave the bushes and the nymphs to abandon their natal leaf, which have implications for whitefly biology, although *B. argentifolii* can move between different crops as they are rotated. Gerling (1999) gives a general review.

5.3.1.2(d) AUCHENORRHYNCHA; Fulgoroidea, Delphacidae. *Nilaparvata lugens*. Brown planthoppers. A widespread Indian and East Asian pest of great importance in rice paddies. Other delphacid bugs of rice. Delphacid bugs comprise >1800 species worldwide, some being major pests of cereals. Indeed, most species feed on monocots, although in North America several others attack Compositae. Many are migratory and in those feeding on low-growing grasses and cereals brachypterous morphs are common. Indeed, wing polymorphism is widespread and may well contribute to the group's success (Denno and Roderick, 1990). Species feeding on trees, however, are usually all macropterous. Levels of nitrogen in food plants have a big effect on growth (White, 1993), and in train on other life-history features. As in cicadas, there is acoustic communication, here comparatively subdued. Since mating normally occurs *after* migration, this facilitates the sexes meeting at low density. Females slit the plant's tissue with an ovipositor and insert small egg batches, covering them with a protective secretion. Even so, nabid and mirid bugs suck them dry, and mymarid and trichogrammatid wasps parasitize them. Dryinid wasps, pipunculid flies and Strepsiptera parasitize the larger nymphs and adults, and many ants, spiders and mirid bugs eat them (Denno and Roderick, 1990). Ants tend some species, protecting them from enemies. Overall, the rapid rate of increase of delphacid bugs, as in the Psyllidae (Section **5.3.1.2(b)**), often results in inversely density-dependent mortality.

Nilaparvata lugens is effectively confined to rice paddies and volunteer plants, which due to spillage are abundant in rice-growing areas. Its feeding, on both xylem and phloem, causes discoloured leaves ('hopper burn') and lodging. It transmits the viral diseases Grassy Stunt, Wilted Stunt and Ragged Stunt (Heinrichs and Mochida, 1984), plus some phytoplasmas (Weintraub and Beanland, 2006). Plants are most vulnerable after planting out at 4–6 weeks old. Females lay ~200 eggs in small batches, often in the leaf sheaths. They hatch in ~1 week. Nymphal development requiring 2–3 weeks, according to temperature, allows several generations annually. Adults of both sexes may be brachypterous or macropterous, the latter condition being induced by crowding in young nymphs, namely density dependence, although nutritional factors such as low nitrogen may have further effects (Cook and Perfect, 1985; Denno and Roderick, 1990). But macroptery has a bias towards males. In resident, tropical regions the proportion of brachypters is high and they are generally less mobile than those that merely overwinter there. Juvenile hormone is probably involved in the development of the brachypterous morph (Iwanga and Tojo, 1986). In the field, the proportion of either morph is best estimated in the final nymphal instar, since this avoids bias caused by early emigration of winged adults, which may comprise up to 70% of the bugs. We note (Section **11.4.2**) that parasitism may be underestimated by a similar error when deaths occur before sampling.

Its increasing importance as a pest follows the misuse of insecticides (Sigsgaard, 2007), especially diazinon, which kill its natural enemies, particularly spiders, preferentially. Since *N. lugens* feeds at lower levels much applied insecticide misses them. In 1977, the zealous application of diazinon in Indonesia resulted in the loss of >1 million tonnes of rice, enough to feed 2.5 million people for a year (Kenmore, 1991, in Ives and Settle, 1997). A similar effect, among many others, occurred with the misuse of endosulphan to kill the coffee berry borers in Jamaica (see Sections **5.2.2.1(b)** and **6.3.1.1(b)**). But high-yielding rice varieties, used from the late 1960s, show less natural resistance to attack, so being a contributory reason for the great increase of *N. lugens* (Kisimoto and Sogawa, 1995). Resistant cultivars (IR36 and IR42) considerably depress its density (Kartohardjono and Heinrichs, 1984) and may act synergistically with natural predation. But apart from killing the pest's enemies, several insecticides, especially decamethrin, stimulate surviving *N. lugens* females to greater reproductive output (Heinrich and Mochida, 1984). On susceptible varieties (IR29), they estimated population increases of >70-fold, whereas on resistant ones (IR42), this 'resurgence' was only fivefold. These are extreme values but some insecticides from all major classes (Section **13.2.3.2**) were found to have a similar effect. More recently, insecticides belonging to the neonicotinoid and phenylpyrazole groups have been used in South-East Asia, but resistance to them is becoming widespread (Matsumoto *et al*., 2013).

Although several rice varieties resistant to this pest have been developed, the general problem is that susceptible ones have the highest yield, and vice versa, the principle of *yield penalty* (Section **2.4.2**). Resources the plant puts into self-protection it cannot put into crop production, recalling Fisher's Fork (Section **9.7**). But Foyer *et al*. (2007), following Mole (1994; Section **2.4.2**), have scrutinized this principle; the metabolic engine of photosynthesis rarely runs at full throttle. If nutrients and water are adequate, annual crops at least can synthesize secondary compounds without affecting yield. Also, *Bt* rice expressing genes Cry1ab, together with several promoters, have insignificant effects on *N. lugens* and its mirid predator *Cyrtorhinus lividipennis*, and those transformed with the *gna* gene from snowdrops deliver increased mortality to this pest (Bernal *et al*., 2002).

Like several cicadellid bugs, such as *Empoasca fabae* (Section **5.3.1.2(a)**), the macropterous morphs of *N. lugens* undertake mass, long-distance migration. They can fly for up to 30 hours if the temperature is >16°C (Rosenberg and Magor, 1983). In the laboratory, they have flown for 24 hours, and in wind-assisted migrations high in the air (up to 2.5 km) they may move ~1000 km, while distances of 300–500 km are usual. In China, 850,000 migrants were marked and one of them later found 720 km to the north-east (Rainey, 1989). Low-level jets above the nocturnal temperature inversion often carry them at high densities. By back-tracking weather systems, a method used extensively by C.G. Johnson (1969) and his colleagues at Rothamsted, UK, it was found that *N. lugens* arrives in south-west Kyushu, Japan (~33° N), from sources including mainland China, Korea, possibly Taiwan (Wada *et al*., 1987; Kisimoto and Sogawa, 1995) and North Vietnam. Major migration routes can be inferred by comparing genetic similarities (Matsumoto *et al*., 2013). Bugs migrating long distances may run out of flight fuel, or desiccate in dry air. But an extraordinary record exists of their landing on the surface of the sea and then *taking off*. There are early summer and autumn migrations in Japan, the former spreading to Honshu, where there are commonly three generations, causing increasingly severe infestations. Over the last century, annual outbreaks there have usually occurred with those of another migrant bug, *Sogatella furcifera*. In some regions, double-cropping rice is unsuitable for migrants due to asynchrony with the pest. Topography affects their landing, higher densities accruing in the lee of hills (Section **10.1.1**). Then there is evidence of southward and westward migrations late in the year, and in China there is a three-stage re-migration in late summer (Cheng *et al*., 1979, in Kisimoto and Sogawa, 1995; Riley *et al*., 1991).

Spiders are major enemies of these bugs in Asia. In China, they include the lycosid species *Pardosa* (=*Lycosa*) *pseudoannulata* and *Pirata subpiraticus*, jumping spiders like *Marpissa magister* and also smaller, web-spinning Linyphiidae, such as *Ummeliata insecticeps*, *Gnathonarium dentatum* and *Atypena formosana* (Zhao *et al*., 2004; Sigsgaard, 2007), that tend to consume young nymphs. In the Philippines, *P. pseudoannulata* and *A. formosana* are major predators, where under experimental conditions, Sigsgaard found that mutual predation within the predatory guild could engender greater control of *N. lugens*. The eggs and young nymphs are sucked dry by *C. lividipennis* and *Tytthus chinensis* (Miridae) and the aquatic *Microvilia douglasi* and *M. atrolineata* (Veliidae) (Heinrichs and Mochida, 1984; Kuno and Dyck, 1985; Cook and Perfect, 1989). These mirid bugs together with spiderlings have been captured with both delphacid pests in migrant swarms to the south-west of Japan (Kisimoto, 1984). The mymarid wasp *Anagrus* sp. parasitizes the eggs, and the dryinid wasp *Dicondylus indianus* is one of few nymphal parasitoids.

Nilaparvata lugens is the major pest in the Ganges region and in Sri Lanka. Since re-migration in autumn is often weak, while the species is generally incapable of overwintering north of the 25° parallel, it provides a case of apparently non-adaptive movement (Section **10.2.4.1**). Kisimoto and Sogawa (1995), however, argue logically that even a small proportion of re-migration would be sufficient to make redistribution adaptive. Most insects live in a very hazardous world. *Nilaparvata lugens* is also found in Thailand and adjacent countries, and in Indonesia, New Guinea and Queensland, Australia. Several other species of *Nilaparvata*, including *N. bakeri*, *N. muiri*, *N. albotristriata*, *N. lineolae* and *N. castana*, are found in South-East Asia, but none of them attacks rice (Kisimoto, 1984).

Another delphacid bug, *Sogatella furcifera*, the white-backed plant-hopper, is also a serious pest of rice and maize in the same region and migrates in a similar way to *N. lugens*, although only the females show alary dimorphism. It occurs sporadically on young rice plants and may vector Rice Yellows and Stunt Viruses. Conversely, its feeding induces resistance in rice to blast fungus, *Magnaporthe grisea* (Kanno *et al.*, 2005, in Stout *et al.*, 2006). But rice can respond to its oviposition by forming a neoplasm that lifts the eggs from the plant's surface, and may produce the ovicide benzyl benzoate (Seino *et al.*, 1996). Even so, *Sogatella* is less affected by resistant cultivars than *N. lugens* and thus remains as food for those predators it shares with this bug (Kartohardjono and Heinrichs, 1984), another probable case of *trans-specific mortality* (Section **10.2.3.9**). The polyphagous and migratory *Laodelphax striatellus*, which transmits MRDV virus, is a minor pest there, while *Zygina maculifrons* is recorded from India (Mani and Jayaraj, 1976, in Heinrichs and Mochida, 1984). For greater detail of viral vectors of rice see Table 3 in Kisimoto (1984).

5.3.1.2(e) AUCHENORRHYNCHA; Fulgoroidea, Delphacidae. *Perkinsiella saccharida*. Sugar cane plant-hoppers. Pan-tropical pests of sugar cane. Several Auchenorrhyncha attack this crop, including the cercopid bug *Aeneolamia*, (Section **3.3.2.1(b)**), plus two delphacid bugs, the present species and *Saccharosydne saccharivora* (Section **5.3.1.2(f)**). While *P. saccharida* is pan-tropical (Box, 1953), not all countries in this belt are affected. Nowhere is it presently serious. It originated in Queensland and on reaching Hawaii, at the beginning of the last century, caused considerable damage until it was brought under control by importing natural enemies. It is common in the West Indies and found in Florida, USA, in 1982. It has ~six generations per year, that is, on a single cane crop. Its attack causes reddening of the leaves and in severe cases the spread of sooty moulds. It transmits the virus causing Fiji Disease. Females deposit several eggs in incisions in the midrib, leaf blade or sheath. AF is ~300 and development takes 7–8 weeks. As in the preceding species there are apterous and winged morphs. A major predator of the eggs is the mirid bug *Tytthus mundulus*, while adults may be parasitized by *Elenchus* spp. (Strepsiptera). *Perkinsiella vitiensis* is found in the Fijian Islands.

5.3.1.2(f) AUCHENORRHYNCHA; Fulgoroidea, Delphacidae. *Saccharosydne* (= *Delphax*) *saccharivora*. Sugar cane plant-hoppers. Some other Neotropical delphacid pests and disease vectors. Metcalfe (1968, 1971) studied this species extensively in Jamaica and Belize, recording historical, sporadic outbreaks there from the 1750s. It may form outbreaks in the Greater and Lesser Antilles, Mexico and Venezuela, but although their causes are unknown they have been linked to climatic factors, to natural enemies and to the misuse of insecticides. Another odd feature is that the several annual generations are synchronized over areas of at least 1000 ha. A variety of wild grasses in open situations also provides adult food, while they also feed on *Andropogon glomeratus* and *A. bicornis*, which may have been the original food plants before cane was introduced.

Eggs, in elongated batches of 6–8, are inserted into the midrib of the leaf, which becomes necrotic and red, providing a diagnostic trace. They hatch in an extended period of 13–23 days (Metcalfe, 1968). The nymphs through five instars take ~2–3 weeks to reach adulthood, males developing slightly faster and being slightly smaller. On unfertilized ratoon cane development is longer. Males live only 1 week compared to 4 weeks for the females. In heavy infestations the cane may become matted with the black fungus *Capnodium* growing on honeydew spillage. Chrysopid, coccinellid and ant predators attack all stages. *Tetrastichus* (Eulophidae) and *Anagrus* (Mymaridae) parasitize the eggs. The stylopid parasitoid, *Stenocranophilus quadratus*, afflicts the nymphs and adults and may affect >80% of them. This equates with even greater mortality or sterilization (Sections **8.2.2.5(c)** and **11.4.2**; Van Driesche, 1983). But there is considerable variation between fields and host generations. The AF of *S. quadratus* is ~1000 and its victims are often multiply parasitized. Metcalfe found in a large sample of adult female hosts that only 4% contained mature eggs. In wet weather the fungus *Metarhizium anisopliae* is a common pathogen. Denno and

Roderick (1990) and Denno and Perfect (1994) give reviews of the population biology and control of these bugs.

Delphacodes kuscheli breeds on winter wheat, oats and rye in Argentina (Grilli and Bruno, 2007). It is important as a vector of Rio Cuarto disease of maize, on which it does not breed. As in *N. lugens* short- and long-winged morphs exist, migration occurring between crops. *Hyalesthes obsoletus* (Cixiidae) is another fulgoroid bug recently spreading in Europe. The adults feed on grapevines but breed on the roots of some wild plants that vary regionally (*Convolvulus arvensis*, *Urtica dioica*), namely a diverse resource base exists (Johannesen *et al*., 2008; Section **13.1.2.2**). Its distribution is also influenced by MAP and soil type (Panassiti *et al*., 2013). It transmits grape yellows disease (or bois noir), a phytoplasmal disease of the stolbur group (Lee *et al*., 2000; Weintraub and Beanland, 2006). Over the last 10 years both the bug and bois noir have become common in Germany, congruent with the spread of *U. dioica*. The recent spread in Europe from the USA of the flatid bug *Metcalfa pruinosa*, is similarly related to this plant.

5.3.1.2(g) STERNORRHYNCHA; Aphidoidea, Phylloxeridae. *Phylloxera* (= *Daktulosphaira*) *vitifoliae* (= *vastatrix,* = *Viteus vitifoliae*). Grape phylloxera. A devastating scourge of European grapes. While many true aphids alternate between winter and summer food plants and sexual and asexual reproduction, this pest afflicts several species of grapes, the alternation, if any, being between root and shoot system. Even so, extensive studies using molecular markers (Vorwerk and Forneck, 2006) suggest that the main mode of reproduction is asexual although all *Phylloxera* female morphs lay eggs (Blackman and Eastop, 2000). *Phylloxera vitifoliae* was carried from North America to France and Germany in 1874 or earlier (Balbiani, 1874, in Forneck and Huber, 2009), the reverse of normal proceedings, and subsequently to South Africa and Australasia. In the latter part of that century it became the scourge of the French wine industry, then one of the largest in the country since in various capacities it employed a commendable 15% of the national work force. There are several closely related, resistant American species of vine and one of these, *Vitis rupestris*, was hybridized with the susceptible European vine (*V. vinifera*) to produce the variety AXR no. 1. Such an approach is fraught with danger since a cultivar too close to the original, highly susceptible one may allow a new biotype of the pest to adapt to it: one foolishly makes a biological bridge. This duly happened in 1914, the French growers having ignominiously to opt for 100% American rootstock, which is used today (Thacker, 2002). Similarly in Jamaica, when the phytoplasma causing lethal yellowing had all but wiped out Jamaican Tall coconut plantations, some bright spark had this original cultivar crossed with the resistant Malayan Dwarf. This cross is presently being destroyed by the phytoplasma, faithfully transmitted by its cicadellid vector (Section **5.3.1.2(a)**). Now even Malayan Dwarf coconut palms are succumbing to it (Brown *et al*., 2006). Such are the evils of not understanding even a modicum of evolutionary theory. In well-tended European vineyards with American rootstocks *Phylloxera* is seen rarely, but abandoned vineyards may harbour them.

Phylloxera is among the more advanced homopteroids. Here we begin to see diverse complexities in the life cycle. The complete cycle generally occurs only on American vines, while on European ones generations on the roots are emphasized. In vineyards away from their native range, *Phylloxera* tends towards asexuality (Corrie *et al*., 2002), as in Australia. Unlike that in most aphids, the alternation of generations takes place on the same plant: several generations produce pocket-like galls on the leaves followed by more on the roots, causing splits and crater-like cankers. These allow the entry of lethal pathogens. Soil type has effects: clays, with their great retention of moisture, are associated with more severe outbreaks than are sandy soils. Females have an AF of ~200, but temperature is influential. In California many eggs fail to hatch at <16°C and >36°C. Nymphs survive best at 21–28°C, while adults die above 32°C (Granett and Timper, 1987). There may be up to ten annual generations and a single mature vine may support over a million of these bugs, causing its slow decline (Granett *et al*., 2001).

First, winged *sexuparae* arise from *radicicolae* on the roots. Crawling up from these nether regions these alates (see the figure on p. 498 of Hamilton, 1996) fly off seeking the aerial parts of other vines where they produce the small sexual forms. So other vineyards become infected. As in *Pemphigus* (Section **3.3.3.1(a)**), the oviparae lay only single eggs (Forneck and Huber, 2009). From these, *fundatrices* develop leaf galls, in which they lay many asexual eggs. These hatch into *gallicicolae* that initiate more galls and lay more eggs. As summer progresses these increasing progeny drop to the ground and become egg-laying radicicolae, which produce either more gallicicolae or, especially in the USA, winged sexuparae. But, as these authors and Corrie *et al.* (2002) point out, considerable reproductive variation exists, the latter authors warning that infected rootstocks are the most likely source of new infestations. In this connection, several clone lineages exist that vary in their biological characteristics (Herbert *et al.*, 2010).

5.3.1.2(h) STERNORRHYNCHA; Aphidoidea, Aphididae, Aphidinae. Aphids as a group are ~200 million years old (Moran, 1992b) and today comprise ~4500 species (Blackman and Eastop, 2000). They are a small family with a big impact, largely due to their transmitting plant viruses, and easy to recognize as they bear dorsally a pair of odd tubes, the cornicles (= siphunculi), near the end of the abdomen. When their parthenogenesis and intricate polyphenism arose is unknown, although fossils show that viviparity occurred in some Cretaceous species. We dealt with some complexities of aphid life cycles for *Pemphigus* in Section **3.3.3.1(a)**. Briefly, in summer there are several alate or apterous generations of parthenogenetic females, the latter often having enhanced AF. In holocyclic aphids (q.v.), low temperature and reducing day length in autumn induce the winged sexual forms. Using *en masse* scanning (q.v.), these locate woody, winter food plants to which they tend to be more specific than to the summer ones. They overwinter as diapausing eggs that hatch in spring to give wingless, asexual *fundatrices*. The production of sexual forms in spring is prevented by an innate mechanism, the *interval timer* (Lees, 1966). In anholocyclic species the sexual phase is absent. Their parthenogenesis is a far-*r* strategy: embryonic offspring start to develop even before their mother is born, telescoping the generations and promoting a rapid increase in numbers (Section **9.1**). Originally it was thought that in producing clones by parthenogenesis they had forfeited variability. Loxdale (2007) and others, however, have shown that complex genetic mechanisms permit adaptation to local conditions even in the asexual phase, indeed they may have variable morphs and behaviour (Schuett *et al.*, 2015). Aphids are one of the few groups that are more diverse in temperate regions, where they are major pests, than in the tropics (Dixon *et al.*, 1987; Cammell and Knight, 1992; Dixon, 1998). Most species are north temperate and highly researched (Blackman and Eastop, 2000). But several of these are also present in tropical uplands (Nair, 2007), and there are some truly tropical pests such as *Toxoptera*, the citrus and coffee aphids.

Here we consider the bulk of economically important species. Aphids often attack apical leaves, hence stunting growth. They probe any plant on which they land, an iterative searching for food that makes them efficient vectors of numerous viruses and compounds the direct damage they cause. Most viruses are stylet borne, but this spreads them on only a restricted spatial scale, as the virions soon die. Persistent viruses, such as Potato Leaf Roll, are spread by long-distance migrants (Ossiannilsson, 1966; Dixon, 1998). Like most other Hemiptera, aphids insinuate their mouthparts between the cells to tap into the plant's phloem (Gauld *et al.*, 1992), but some take sips from the xylem (Dolling, 1991). Although doing little damage to the tissues, which could quickly elicit a defensive response, plants are still able to react to the bug's saliva. This contains peroxidases and pectinases, which are the probable elicitors of the plant's defensive response (Howe and Jander, 2008; Section **2.4.2**).

Aphids generally have no natural, definable habitat, excepting when their food plants are restricted to a particular biotope (cf. pierid butterflies; Section **5.2.1.4(k)**). Some species such as *Aphis fabae*, *A. gossyppii* and *Myzus persicae* affect many plant species in summer and we provide ideal habitats for them in field and orchard crops. Aphid parasitoids belong to two specialized groups. In the Braconidae, Aphidiinae, *Aphidius*, *Trioxys*, *Diaeretiella* are important genera, while in the Chalcidoidea, Aphelinidae we note *Aphelinus* and *Encarsia* (Starý, 1970; Section **8.2.2.5(m)**). These support diverse hyperparasitoids (Sigsgaard, 2002), which largely affect *Aphidius*. They include *Alloxysta* and *Phaenoglyphis* (Alloxystidae), *Asaphes* and *Coruna* (Pteromalidae) and *Dendrocerus* (Megaspilidae). Such hyperparasitic wasps are important as they may compromise biocontrol programmes, but their natural dynamics are extremely poorly known (Sullivan and Völkl, 1999) as, indeed, are those of their hosts (Section **11.4.4**).

Aphids also fall prey to many predatory arthropods: larval syrphid flies, adult dolichopodid flies, lacewings, carabid and coccinellid beetles and linyphiid spiders (Sunderland *et al.*, 1986). But these enemies often have little effect in restraining numbers until the end of the growing period (Dixon, 1998), when it is too late to be useful. The fungus *Erynia neoaphidis* may attack aphids, a single cadaver producing thousands of spores. Their rate of increase on individual plants is promoted largely by high levels of phloem amino acids (White, 1993; Dixon, 1998). This occurs either when leaves are being built, or in deciduous trees, just before leaf abscission in autumn. Aphids are also affected by the spectrum of amino acids in the plant (Gündüz and Douglas, 2009). They possess symbiotic *Buchnera aphidicola* γ-proteobacteria (Douglas, 1998; Oliver *et al*., 2008) that assist viral transmission and provide them with essential amino acids. In some morphs these symbionts comprise an amazing 10% of body weight. Apart from such *obligate symbionts* some aphids possess *facultative bacterial symbionts* that may help them survive heat stress (Montllor *et al*., 2002). Other bacteria, like *Hamiltonella defensa*, arm them against parasitoids (Dale and Moran, 2006). But in *Acyrthosiphon pisum*, this bacterium reduces parasitism by *Aphidius ervi* and speeds up development too (Oliver *et al*., 2008). Other data (Dykstra *et al*., 2014, in Asplen *et al*., 2014) show that its presence entails a fitness cost to the aphid, while its global distribution is patchy. Associated phages are also involved. *Regiella insecticola* permits several aphids to increase their spectrum of food plants (Tsuchida *et al*., 2011, in Feldhaar, 2011). We recall that temperate pest aphids tend to be polyphagous during summer. Another symbiont, *Arsenophonus*, is found in *Aphis glycines*. For many reasons, but especially nutrition, symbionts are of key importance in aphid biology.

As well as having structurally different morphs (Section **3.3.3**), several aphids (*Myzus nicotianae*, *Acyrthosiphon pisum*, *Sitobion avenae*) have green and red/brown colour forms which show different physiological and behavioural characteristics, recently dubbed ‘personalities’. The red morph often does well when crowded in summer. But in *Ac. pisum* it is vulnerable to the ladybird *Coccinella septempunctata*, while the green form is more often parasitized by *Aphidius ervi* (Losey *et al*., 1997). These aphids also have behavioural types that drop or stay on the plant in the presence of coccinellid beetles (Schuett *et al*., 2015). Green/red polymorphism is also known in an African flatid bug (Richards and Davies, 1988), individuals of both colours arranging themselves in the form of an inflorescence.

Myzus persicae has developed some genetically based forms that are extremely resistant to insecticides, which of course are applied mainly during summer (Section **13.2.3.4**). These forms survive the winter poorly, so balancing selection maintains the polymorphism. Another odd morph, which occurs in a few pemphigine aphids, is a soldier female functioning to defend the colony, and may or may not reproduce (Aoki, 1977). In an odd reversal of expectation, aphids have occasionally been found feeding on the eggs of their predators, including those of *Chrysopa* and coccinellid beetles. They also have a taste for cannibalism (Banks *et al*., 1968), a behaviour that is more common when plant food is inadequate. Having dealt with root-infesting aphids in Section **3.3.3**, we now review the remainder.

5.3.1.2(i) STERNORRHYNCHA; *Aphis fabae*. Black bean aphid. An almost cosmopolitan pest attacking legumes, sugar beet and potatoes. This aphid can be found from Northern Europe to the highlands of Africa, but is absent from the Far East and Australasia. In temperate Europe, it is holocyclic: its winter woody food plants being spindle trees (*Euonymus*) and wayfaring trees (*Viburnum*). In summer it attacks mainly legumes and annual weeds. Worldwide it is the most damaging pest of faba beans; >6000 individuals have been counted on a single plant. But such alternation of food plants, while common in major pests, is found in only ~10% of all aphid species. The strategy probably arose in the Tertiary with the contemporary radiation of herbaceous angiosperms (Moran, 1992b). A factor for alternating their food plants may be that most tree species have low levels of phloem amino acids in summer, but have spring and autumn peaks of these foods. Apterous *fundatrices* hatch from winter eggs and produce *fundatrigenae* parthenogenetically. In *A. fabae* winged *migrantes* females then fly to various summer food plants: beans and peas (Papilionaceae), sugar beet (Chenopodiaceae), and weeds such as poppy (Papaveraceae) and dock (Polygonaceae). Summer generations are either apterous or alate *alienicolae*. The latter move between different but related plants (Gatehouse, 1997), spreading the same virus to all of them. Thus they spread Beet Yellows and Beet Yellow Net Viruses, but also inject toxins into the plant (Lange, 1987). Summer morphs are always parthenogenetic.

Early summer infestations are very damaging because crop plants are small. By August the populations of aphid predators such as coccinellid beetles and syrphine larvae, and parasitoids such as *Aphidius* and *Praon*, begin to catch up. Even so, densities may exceed 200 million/ha on sugar beet.

The *sexuparae* fly in search of winter trees, where they give birth to apterous female sexuales, which are mated by winged males. They lay several eggs in convenient niches on the twigs. In the UK, while egg densities on spindle trees are a good predictor of next season's pest population (Jones and Jones, 1984), this does not take account of any mass migrations from continental Europe, which workers at Rothamsted found to be often important. Indeed, Way *et al*. (1981) had already shown a significant correlation between the aerial density of migrating *Aphis fabae* and the subsequent percentage infestation of bean plants (Leather *et al*., 1993, p. 178). This is not contradictory: population size may be correlated with several factors.

Aphis glycines has recently become a pest of soya beans in north central North America and because it occurs widely in Asia, for example from Jilin, China, to Indonesia, it is expected to spread. Although parasitoids attack it, they fail to restrain its numbers. A population of the anthocorid bug *Orius insidiosus* (Section **8.2.2.3(c)**), however, was found to do so, providing it was present early in the season, a good example of Forrest's maxim (Section **10.2.5.2**). *Aphis craccivora* is small and black and found on cowpeas and groundnuts and various other legumes. It transmits >30 viruses and is generally anholocyclic (Blackman and Eastop, 2000). There is a variety of lesser-known congeneric pests, including *A. pomi* on apple, *A. citricola* and *A. spiraecola* on citrus, the cosmopolitan *A. gossyppii* on cotton and *A. nerii* on oleander, a particularly poisonous shrub. Both *A. spiraecola* and *A. gossyppii* transmit Tristeza Virus of citrus (below). *Chromaphis juglandicola* is found on walnut trees.

5.3.1.2(j) STERNORRHYNCHA; *Acyrthosiphon pisum*. Pea aphid. A generally widespread, temperate pest of legumes. These aphids are quite big, 2.5–4.4 mm long, and normally easily identified by their green bodies and red eyes. The species is confined to legumes, particularly field peas, but also clovers and lucerne, although it does not attack *Phaseolus* (Davidson and Lyon, 1986). Originally Old World, it reached North America in the late 1800s. Considerable damage is often caused to pea fields by this species (Soroka and MacKay, 1990), and it has different strains adapted to the different cultivars of lucerne, including the North American alfalfa. Among >30 viruses it transmits Pea Mosaic, Pea Leaf Roll, Bean Yellow Mosaic and Lucerne Mosaic Viruses. Winter eggs are laid on standing forage crops such as lucerne. In the USA, sexual forms occur only in northern states, in the south asexual reproduction continues. This aphid has an aphidiine parasitoid, *Aphidius ervi*, which has been used in biocontrol (Powell and Wright, 1988; Snyder and Ives, 2001), while an established congeneric wasp, *Aph. smithi*, is ineffective. Pea cultivars such as Pride and Onward show resistance, which is generally the case in those with low amino-acid levels. The species is a complex, but usually confined to legumes (Peccoud and Simon, 2010, Table 1). Several other congeneric species are also found on leguminous plants. *Acyrthosiphon kondoi* is now widely distributed and can be troublesome on lucerne, while *A. solani* is sometimes found on solanaceous crops and wild plants.

5.3.1.2(k) STERNORRHYNCHA; *Myzus persicae*. Peach/potato aphid. A broad-spectrum, cosmopolitan pest and pernicious virus vector. Holocyclic *Myzus* spp. often associate with *Prunus* during winter (Blackman and Eastop, 2000). *Myzus persicae* is the pre-eminent vector of plant viruses (Dixon, 1998). This is because (i) it attacks a wide variety of summer food plants, including potatoes, tomatoes, swedes, beet, spinach, turnips and other brassicas, and many weeds; and (ii) the habit of the alate females of moving low down from plant to plant during the summer generations, when they feed on both infected and uninfected plants. In this connection the alates have large wings in relation to their body size. Its mobility means that its densities rarely build up, so direct damage is also rare. Syrphine larvae and the parasitic wasps *Aphelinus* spp. and *Diaeretiella rapae* are among its main enemies, while *Aphidius matricariae* has also been recorded (Wool *et al*., 1978). Of the >100 viruses *M. persicae* is known to transmit we list:

A. Leaf Roll, Ring Necrosis, Yellow Dwarf and A, C, M, S, X and Y Viruses of potatoes.
B. Mosaic, Mosaic Yellow Net and Yellows Viruses of sugar beet.
C. Cauliflower Mosaic Virus.
D. Cabbage Black Ringspot and Ring Necrosis Viruses.
E. Onion Mosaic and Yellow Dwarf Viruses.
F. Celery Mosaic Virus.
G. Cucumber Mosaic Virus.
H. Sugarcane Mosaic Virus.
I. Sweet Potato A Virus.

In tomatoes, *Lycopersicon esculentum*, genes introgressed from *L. pennelli* can provide resistant cultivars having a variety of trichomes on their leaves (Kennedy, 2003). Crawling aphids like *M. persicae* and *Macrosiphum euphorbiae*, and other small bugs such as whiteflies, become entrapped in these structures, while their broken tips release toxins and phenolics such as rutin. The latter substances polymerize proteins making them of little food value.

In *M. persicae*, the sexuales lay only 5–10 eggs per female. In the absence of peach or plum trees as refuges, they overwinter as parthenogenetic apterae on biennials, such as some brassicas. They can survive sub-zero temperatures, reproducing slowly in mild weather and moving upwards from older pre-senescent leaves (Harrington and Taylor, 1990). Even so, considerable mortality can occur, the LD_{50} (Section **10.2.3.3**) being about –8°C to –12°C according to previous conditions experienced. In glass-houses they attack chrysanthemums and may overwinter there. They also overwinter on stored potatoes or onions. Taylor (1977), in the Rothamsted Insect Survey, studied the seasonal migrations of this aphid in the UK. An overwintering nucleus of population exists in the lower Thames Valley, where the weather is relatively mild and from which colonization of the rest of the UK takes place in late spring. Winter survival is probably limited in the west by high rainfall and in the north by low temperature. *Myzus cerasi*, the black cherry aphid, is recognizable since its legs and antennae are banded with yellow. It transmits wilt and decline disease of cherries. As is commonly the case its summer food plants are various, although here these may relate to sibling species. *Phorodon humuli* also overwinters on *Prunus*, where it does little damage, but the summer generations on hops may disrupt growth, spread honeydew and hence sooty moulds.

5.3.1.2(l) STERNORRHYNCHA; *Brevicoryne brassica*. Cabbage aphid. A cosmopolitan pest and virus vector of brassicas. For this important pest from a small genus, brassicas are the only food plants. But it may attack a few cruciferous weeds such as charlock, *Sinapis arvensis*, providing alternative food (Hughes, 1963), as does volunteer rape, although lightly infested (Blackman and Eastop, 2000). Turnips are almost immune. Colour is an important initial attractant: red cabbages elicit no settling response. In train, it is the possession in brassicas of the mustard oil sinigrin that elicits feeding. The bulk of the population is comprised, as in most aphid species, of apterous, parthenogenetic females whose reproductive rate is inversely proportional to their degree of crowding. Winged, parthenogenetic females, induced by crowding of the nymphs, are produced periodically after mid-summer and during autumn. They may occur in vast numbers and spread the infestation, but apterae and eggs can also be transported with the marketable product. Winged males occur occasionally, and there may be up to 20 generations/annum (Eastop, personal communication).

In cool, temperate countries many brassicas are biennial. With the approach of winter, apterous oviparae lay eggs on the persistent cabbage stems, usually near the leaf scars where they gain attachment. In very cold countries, such as Finland, the entire population passes the winter in this stage. In milder regions, such as France, as one moves south progressively more apterae can survive winter and even slowly reproduce, particularly within compact brassicas like savoys and cauliflowers. In Australia (Canberra) and Israel hardly any winter eggs are produced. Chief predators are syrphine larvae (Schneider, 1969). In several areas the aphidiine parasitoid *Diaeretiella rapae* attacks the larger stages, and may itself be attacked by the hyperparasitoid *Alloxysta ancylocera* (Cynipidae) (Sullivan, 1987). In North America, *Lysiphlebus testaceipes* (Braconidae) can be an effective control agent of this aphid. The several aphids attacking cereals from warm to cool temperate regions are now considered. They are still regularly sprayed with insecticides, although specialists feel that they would be restrained advantageously by better IPM using generalized predators (Sunderland *et al.*, 1987; Winder *et al.*, 2005; Section **13.3.2.2**).

5.3.1.2(m) STERNORRHYNCHA; *Diuraphis noxia*. Russian wheat aphid. A largely Mediterranean pest and virus vector of cereals. This aphid originated in southern Russia and the Mediterranean but reached South Africa in the 1970s, North America and Mexico in the 1980s, and latterly South America and Australia. This rapid expansion has occurred despite a battery of parasitoids that attack it, which include *Aphidius colmani* s.s., *A. ervi*, *A. matricariae*, *A. rhopalosiphi*, *A. uzbekistanicus*, *Diaeretiella rapae*, *Ephedrus plagiator* and *Praon volucre* (Starý, 1999). Like *B. brassicae* it has no woody refuge, being confined to the Gramineae. It affects cereals such as wheat, oats and barley and several forage grasses, but resistance to it varies with cultivar and the physical conditions of plant growth. Alates are produced under crowding. Only parthenogenetic reproduction is known and development to the adult takes a week under optimal conditions. The saliva injected during feeding inhibits chlorophyll production, producing whitish or purple lesions along the leaf blade, which rolls up. More mature plants suffer a reduced yield of grain. It transmits several viruses including Brome Mosaic and Barley Stripe Mosaic.

5.3.1.2(n) STERNORRHYNCHA; *Rhopalosiphum maidis.* Maize leaf aphid. A cosmopolitan pest and virus vector of the Gramineae. Some other grain and lucerne aphids. This species attacks maize, sugar cane, grain and grasses and also tobacco, causing mottling of the leaves. Although it is essentially parthenogenetic with winged and apterous forms, males are occasionally encountered. Under ideal conditions the generation length may be <10 days. There is a south to north migration during summer in the Northern Hemisphere, as in *Aphis fabae*. It is a vector of Sugar Cane Mosaic Virus, Maize Dwarf Mosaic Virus and Barley Yellow Dwarf Virus, among many others. Other grain aphids include *Schizaphis graminum*, which like *D. noxia* comes from southern Russia. It lays shiny black eggs that overwinter in the north, but it reproduces continuously in the south. Black eggs are frequent in aphids and may be cryptic and/or protect against UV radiation when exposed (True, 2003). They also occur in *Tipula*. West of the Mississippi River, USA, *D. noxia* is a pest on wheat, oats and barley, having different strains on different crops. In resistant barley varieties at higher temperatures, parasitoids prevent much damage. It may outbreak on non-resistant crops at temperatures <10°C, since its parasitoids require >15°C to function well. Similar relationships to temperature occur: (i) in India between the cabbage aphid *Lipaphis erysimi* and its predator *Coccinella septempunctata*, temperatures <20°C favouring the aphid (Atwal and Sethi, 1963); and (ii) in the USA between *Therioaphis trifolii* form *maculata*, the spotted alfalfa aphid, and its parasitoid *Praon palitans* (Messenger, 1964a). These are good examples of imperfectly density-dependent mortality factors (Section **11.2.2.4**).

Rhopalosiphum padi, which also attacks potatoes, *R. fitchii*, *Sitobion avenae*, *Metopolophium dirhodum* and *Macrosiphum avenae* and several other aphids transmit Barley Yellow Dwarf Virus in Europe, western Asia and North America. This virus is becoming important partly because of the increasing practice of growing cereals continuously, instead of rotating them, but also because winter wheat is now grown extensively. All the major grain crops are affected, including rice and maize and many wild and cultivated grasses. The virus, which has different strains, mainly affects the roots, which causes stunting of the aerial part of the plant. Some aphid species are specifically attracted to infected plants (Stout *et al.*, 2006), and because of the different dispersive and migratory behaviours they possess, the virus may be spread in enlarged patches within a field, to adjacent fields or to far distant ones. Although the numbers of these aphids are partly restrained by several species of *Aphidius*, *S. avenae*, *M. dirhodum* and *R. padi* are consistent pests of winter wheat in many parts of Northern Europe (Thies *et al.*, 2005).

Holcaphis holci affects the pasture grass *Holcus mollis*, reducing its rate of tillering and its competitive ability against other less desirable sward species (c.f. wireworms in Section **3.2.1.2(a)**). *Hyalopteroides humilis* is found on cocksfoot grass, *Dactylis glomerata* (Section **6.2.1.2(e)**). In such grasses, which are used for seed, hay and silage, and also in beetle banks (Section **13.2.4.7**), several cereal aphids and their parasitoids are present producing a complex patchwork of reservoir populations (Section **13.1.2.2**) in the landscape. Finally, we consider the tropical genus *Toxoptera*.

5.3.1.2(o) STERNORRHYNCHA; *Toxoptera citricidus and T. aurantii.* Citrus aphids. Tropicopolitan pests and virus vectors on citrus. These species generally attack plants in the Rutaceae, to which citrus belongs. *Toxoptera aurantii* also attacks tea (Theaceae) in India (Banerjee, 1983). The Rutaceae contains several genera apart from *Citrus*, including *Ravenia* (Satinwood), *Fagara* (Rosewood), and *Amyris* (Candlewood), which may act as alternative food plants. *Toxoptera* are pan-tropical and exist only as alate or apterous parthenogenetic females, although sexual forms in *T. citricidus* are found in Japan. The generation length is only 7–8 days at the optimum for growth (~28°C), although the number of progeny/females steadily declines from ~50 at 10°C to ~10 at the optimum (Section **10.2.3.3** and **10.2.5.1**). But under natural conditions there is a rapid build-up of the clone, particularly during a dry spell after the rainy season. Honeydew spillage is invaded by sooty moulds (Fungi Imperfecti), leading to loss of photosynthetic area. These moulds live externally and have black pigmented hyphae. They belong to a variety of genera such as *Pseudomicrocera* and *Capnodium*. Dimethoate provides a measure of both systemic and contact control of the aphids. In parts of the Caribbean and South America *Toxoptera* transmit Tristeza Virus (*Closterovirus*, Closteroviridae), which slowly kills citrus that have been grafted onto sour orange rootstock. Colonies of *Toxoptera coffeae* strangely stridulate.

Several aphid species attack coniferous foliage including *Elatobium abietinum* and *Cinara fornacula* on spruce and *C. laricis* on larch. *Eulachnus rileyi*, which attacks pine, is a European native, but extends into the East African highlands. *Pentalonia nigronervosa* is the pan-tropical banana aphid. For a fairly recent work on the ecology of this group by a lifelong specialist see Dixon (1998).

5.3.1.2(p) Coccoidea, Pseudococcidae. *Rastrococcus invadens.*

Mango Mealy bug. While many mealy bugs attack stems, *R. invadens* attacks the leaves of mango, citrus, breadfruit, avocados, bananas and other trees in 22 families; even neem trees are attacked, although lightly. They produce copious honeydew (Willink and Moore, 1988), which becomes colonized by sooty moulds, reducing photosynthesis. The bug is pale greenish-yellow adorned with long filaments of white wax. Originating in tropical Asia, and confused with the related *R. spinosus*, it spread to West Africa by 1982, affecting mangoes and citrus. Losses exceeding 80% are recorded from Ghana. Females show a diversity of reproductive patterns, some producing the bulk of offspring in the first 2–3 weeks while others leave this to the period from 4–16 weeks. In all, more than 150 nymphs may be produced. The encyrtid wasp, *Gyranusoidea tebygi* imported from India, attacks the early instars, and has been used to control it. Predators include the coccinellid beetles *Chilocorus nigrita* and *Exochomus* spp., plus the lycaenid larvae *Spalgis pilos* and *S. lemolea*, but they fail to restrain the numbers of this virulent mealy bug.

6 The Insect Pests of Flowers and Fruits

6.1 General Introduction

Modern seed plants are the Angiosperms (>250,000 species) and the Gymnosperms (~750 species). In Angiosperms the flowers and fruits comprise the plant's sexual reproductive system (Section **2.3.2.4**). Gymnosperms usually have male catkins and female cones. Some lower plants like mosses and ferns have an alternation of sexual and asexual forms, called the gametophyte (haploid) and sporophyte (diploid), respectively. But in seed plants the sporophyte has evolved to total dominance in terms of size. Both male and female gametophytes are reduced and represented only by the pollen tube and the embryo sac within the ovary, in each case. In Angiosperms alone asexual reproduction may take place by vegetative means (e.g. suckers, runners), an ability allowing several plants to produce a single patch, as in bamboo. This is a clone, ostensibly a genetically uniform monoculture. Angiospermous flowers usually represent both sexes in the same organ (bisexual), the male part producing pollen and the female part having ovules within the carpel. However, plants bearing flowers of separate sexes (unisexual) also exist and in this case they may be on the same plant (monoecious) or on different plants (dioecious). Most insect pests attacking flowers select bisexual ones.

Since plants are immobile they must employ some agent to move pollen to others of the same species, or in default self-pollinate (Section **8.2.1.1**). Some plants rely on wind for pollination, but a majority attract animals, particularly insects and birds, to do this. Generally, the agent of attraction is visual but scent is also used, especially in night-flowering species. The rewards are pollen and nectar. Flowers are often arranged in clusters, or inflorescences, thereby increasing their attractive ambit. So one supposes that pests attacking flowers have little difficulty in finding them (Hinton, 1973). When pests damage flowers, their attractiveness to pollinators may be reduced (Strauss, 1997). Thus, herbivores of the plant's reproductive system reduce its fitness *directly* by damage, or *indirectly* by loss of attractiveness, so that fruits are fewer or absent. The reproductive system is of higher value to the plant than other structures (Zangerl and Bazzaz, 1992, in Stamp, 2003b). Even so, damage to other parts of the plant may impair its reproductive output.

A fertilized ovule develops into an embryo, which becomes enclosed in a larger structure, the *seed*. This contains metabolic reserves and protective coverings, much like an animal's egg. One or more seeds are contained within a *fruit*, which usually develops from the ovary and carpelary wall. It is essentially a device to effect seed dispersal, sometimes by wind or water, often by a tetrapod. While insects commonly disperse pollen, tetrapods often disperse seeds. Although many insects eat fruits they are usually too small to transport the seeds, and thus of no value to the plant in this respect. Hence, the insect pests of many fruits exploit the plant's device to attract a tetrapod agent of seed dispersal. For example, a fallen apple is designed by evolution to be eaten by mammals such as deer and wild pigs, the indigestible seeds thereby being dispersed and finally passed out with the fertilizer. In relation to this, fruits often lack defensive secondary compounds, especially when ripe, perhaps also making them more palatable to insects (Aluja and Mangan, 2008). For example, there are fruits whose function to the plant is affected by insect attack and those that are not (Fitt, 1990). The former is more likely when flowers or early fruits are attacked, and always when seeds are consumed.

Plants often excise some of their flowers and later on some immature fruits (Stephenson, 1981). Mangoes are a good example. This mechanism regulates the apportionment of available metabolic resources between the numbers of offspring and their average weight and in train, quality (Harper, 1977), again as in animal eggs (Smith and Fretwell, 1974). Naturally, this mechanism often leads to the death of any insects developing in these organs, indeed many plants preferentially shed those that are being damaged. Tetrapods and even herbivorous insects cause similar mortality. We also mention the few pests of coniferous cones here. Apart from the peculiarity of their woodiness, cones may stay on the tree for several years: very different from fruit.

6.2 Pests of Flowers

Several insects are specialized to attack flowers and commonly reproduce therein. Since it is unusual for plants to flower continuously, the life cycle of these beasts is often geared to the flowering time of the plant they attack, so the duration of their food patch is short (Section **12.2.3.2**). Related to this, we find that a majority of flower pests are specific, although a few, like earwigs and some thrips, are general pests. We define pests of flowers, however, as those insects that attack the flower initially, even though the seed or fruit may be eaten subsequently, while pests of fruit attack at some stage in the development of the fruit itself.

If the flowers are destroyed then the fruits and/or seeds will be destroyed. In crop plants damaged flowers usually yield distorted fruits, and if these are marketable, only a low incidence of attack can be tolerated. Since we eat fruits, caution is necessary in any programme of chemical spraying. Other control methods such as trapping, mating disruption and the sterile male technique (SMT; Section **6.2.1.2(c)**) may be appropriate and have often been used successfully. We will separate these pests into biters and suckers, remembering that this distinction relates to the type of damage they cause, and to their potential to transmit viruses.

6.2.1 Biting pests

6.2.1.1 Exopterygota

6.2.1.1(a) DERMAPTERA. Earwigs. Generalized pests of horticultural blossoms, but are also predatory. *Forficula auricularia* is a persistent pest of flowers used in decorative horticulture in temperate regions. Their name comes from the Old English 'earwicga', meaning 'ear-insect'. The justification for this name seems to be the beast's thigmotactic behaviour, a predilection for creeping into small spaces, even occasionally human ears! This is not mere English fancy because the German name is *ohr* wurm and the French name perce*oreille*.

Breeding is within the soil, where the female lays a batch of 20–80 eggs early in the year. They exhibit a primitive form of parental care, licking the eggs and not allowing the young nymphs to stray. Later the nymphs disperse. They are true omnivores: apart from plant tissue, they consume both living and dead insects. They eat aphids and are major predators of codling moth eggs in Sweden (Subinprasert and Svensson, 1988) and other parts of Europe (Blommers, 1994). They also eat the pupae of cinnabar moths in the soil (Dempster, 1982). Omnivory such as this complicates the simplistic concept of trophic levels (Polis and Strong, 1996; Section **10.1.2**). Later in the year, earwigs get into multi-petalous flowers, like roses and dahlias, and chew both petals and stamens, leading to unsightly blossoms. They may bite into ripe fruits such as apples and strew unsightly frass over them. *Forficula auricularia* itself is attacked by the tachinid fly *Triarthria setipennis*.

6.2.1.2 Endopterygota

6.2.1.2(a) COLEOPTERA; Nitidulidae. *Meligethes aeneus*. Rape blossom beetle. These small, shiny black beetles with clubbed antennae have increased in importance with the recent cultivation of larger areas of rape for vegetable oil (Paul, 1988, in Thies *et al*., 2003). This change is most likely a good illustration of the principle that an extensive regional distribution is a primary determinant of local population density (Section **12.3.2.3**; Cornell and Lawton, 1992). A similar situation occurs in another pest of rape, the midge *Dasineura brassicae* (Section **6.2.1.2(k)**), but see below. The family may be related to the Byturidae (Section **6.3.1.1(a)**). Immigrants colonize flowers in the Cruciferae and in the unrelated Compositae in spring, mate and lay eggs. They and their larvae consume pollen and other floral structures, and when mature pupate in the ground. In Saxony, Germany, the proportion of rape flower buds destroyed was inversely proportional to landscape complexity, and hence directly to percentage crop area (Thies *et al*., 2003). Matrix without rape contained large reservoir populations of three ichneumons that parasitize the larvae: *Tersilochus heterocerus*, *Phradis interstitialis* and *P. morionellus*. Parasitism from them may reach 50% at field margins but only 20% deep within the crop. Predators are scarce and, again, parasitism is related mainly to landscape heterogeneity, not host density (Thies and Tscharntke, 1999), so that weedy corridors across rape fields, rather like beetle banks (Section **13.2.4.7**), could give a green method of controlling these beetles (see below). Attack naturally causes reduced seed and oil yield. In Finland, swarms have attacked cauliflowers to an extent that growing them became impossible. But barrier trap crops of a mixture of rape, sunflowers and marigolds, in which the immigrants are killed with insecticide, have restored cauliflower production (Hokkanen, 1991). They can be captured in yellow water traps to monitor populations, but high reflectance of ultraviolet (UV) is also a factor (Döring *et al*., 2012).

6.2.1.2(b) COLEOPTERA; Curculionidae. *Apion dichroum* (= *flavipes*), *A. apricans*. Clover seed weevils. Monophagous temperate pests. *Apion dichroum* affects white clover and *A. apricans* red clover. These weevils occupy a rather similar position biologically and economically to the cock's foot moth (Section **6.2.1.2**(e)), despite them being in a different order. Both white and red clovers are sown to improve pasture, particularly because, like lucerne, they are legumes and hence fix nitrogen in their roots, which is eventually added to the soil. Red clover is also attacked by *A. aestivum* and *A. virens*, the latter being a stem borer.

In the extreme south-east of England, where the climate is more continental, white clover, *Trefolium repens*, is grown for seed, although less commonly than previously. It is a lucrative undertaking that requires close attention and innate agricultural skill. Clover is normally grown with rye grass (*Lolium*), also for seed. During late autumn and winter, sheep graze the pasture. In April or May more sheep may be needed as the sward can grow faster than the sheep can eat it. This tactic prevents the development of clover flowers at too early a date. Then, on a critical day in late May, that the farmer judges by experience and depends on the state of the field and the prevailing weather, the sheep are removed to hill pastures. Within a week or so the field becomes a solid white carpet of blossoms. Pollination is now the problem. Hives of bees are moved in for this purpose, and a subsidiary crop of clover honey collected. Since by this practice flowering is made to be synchronous in all plants, ripe seed is produced synchronously: that is the aim of the exercise. Were there to be a greater spread in the time of ripening, early ripening seed would fall and late-ripening seed would be immature, factors that would reduce the amount and quality of the seed harvested.

The life cycle of this weevil must be understood in relation to this specialized agriculture, and has probably evolved with it. In late summer, the newly emerged generation feed briefly on clover leaves before flying to woodlands to hibernate. A majority strangely settle on tree leaves and remain there until they fall. But there is a strong tendency to select the litter of specific tree species, for example litter under hazel trees is favoured (Section **9.9**). As the temperature falls the weevils become negatively phototactic, slowly penetrate deep litter and here they overwinter (Freeman, 1965). This movement takes advantage of the higher and less variable temperatures that exist in woodlands compared to open, exposed fields. In this case the difference in minimum temperature is ~5°C. Other pest weevils in *Sitona* and *Ceutorhynchus* are often found in the same situation.

Weevils brought to the laboratory during winter feed on clover leaves offered to them and rapidly lose their ability to resist low temperatures. In nature, warm spring weather (~17°C) induces flight to the fields, where adults search out clover plants and feed on the leaves. At this stage, however, they are still capable of flying. When flowers are produced, weevils feed on them, particularly on the stamens, which are rich in protein. A physiological surge of protein probably induces the atrophy of the flight muscles, which in females are apparently rebuilt into the ovaries. Indeed, the expanding ovaries come to fill the space formerly occupied by the flight muscles in the thorax, so that a metabolic store functioning for *dispersal* is converted to the needs of *reproduction* (Section **9.7**). Hence, females are capable of rapid oviposition. At peak flowering a rate of ~10 eggs/female/day is achieved, although the normal rate is only 2–4 eggs/day (Freeman, 1967a).

Clover flower heads comprise 30 or more florets, each with a pod-like ovary. A single egg is laid in each pod. Ideally for the weevil, each pod provides enough food for the complete development of one larva. Larvae are rarely parasitized, but the pupae, which remain within the dead flower, are attacked by the eulophid wasp *Entedon* spp. Their black, flattened pupae, together with those of *Apion,* are easily visible in seed samples. At the end of the reproductive period the flight muscles are reconstructed and surviving old females fly back to the woodlands. In dissected samples they may be distinguished from young ones by the state of their ovaries. In spring, these old ladies fail to fly again and eventually die. The overall annual ambit of movement of the *majority* of weevils is probably ~200–300 m. *Adults* are parasitized in autumn and in the following spring by the braconid wasp, *Microctonus* sp. near *aethiops*, whose method is to insert the ovipositor into the base of the antenna, although the 'fluid' egg comes to rest in the abdomen. Several species of *Microctonus* (meaning the 'little destroyer') attack the *adults* of other weevils (Loan, 1963; Harcourt, 1990), flea beetles (Smith, 1952, in Salt, 1968) and carabid beetles (Luff, 1976), who may transport them (see Section **8.2.2.5(m)**). Other such parasitoids of these adult weevils are *Centistes lituratus* and *Pygostolus falcatus* (Jackson, 1920; Loan, 1963).

Intense attack by weevils reduces seed yield by ~35%, turning a handsome profit into a miserable loss. Clover can be sprayed with a short-term insecticide, such as malathion, just as it is coming into flower, about 5 days before hive bees are brought in (Freeman and Wimble, 1970), a strategy taking advantage of the fact that the weevils have lost their flight capacity. This kills most of the *Apion* in the fields, while the residual population on hedgerow and wasteland clover, now being flightless, can no longer migrate onto the crop. But timing is critical. If it is too early not all immigrants will have arrived; if it is too late pollination is debarred until the insecticide has dissipated. Today trials with *Bacillus popillae*, which targets beetles, should be undertaken.

Apion onopordi affects the thistle, *Cirsium arvense*, transmitting the rust fungus *Puccinia punctiformis*. Weevils feeding on infected thistles are larger, survive better and are more fecund (Bacher *et al*., 2002, in Stout *et al*., 2006; Section **10.2.2.5**).

6.2.1.2(c) COLEOPTERA; Curculionidae. *Anthonomus pomorum*. Apple blossom weevil. A monophagous pest in Europe and North America. Apples, *Malus pumila*, are of Asian origin, not cultivars of European crab apples, *M. sylvestris* (Alford, 2007). This blackish weevil, ~6 mm in length, recently resurged as a pest in parts of Europe. It is also of interest because of the oddities in its life cycle. The adults overwinter in sheltered places, such as under flakes of bark on apple and other trees, but also like *Apion*, in leaf litter at the edge of woodlands or in grass tussocks. They fly into orchards in early spring (Toepfer *et al*., 1999), even at temperatures <10°C (~17°C for *A. dichroum*), tending to concentrate on peripheral trees. They respond to volatiles from the unfolding leaves, mate, and feed on the buds and developing flowers. Females bore these flowers and deposit single eggs. The young larva bites through the base of each petal, preventing opening and producing 'capped blossoms' (Miles, 1923). This is complex behaviour for such a small insect, one that must be innate and 'hard-wired' into its minuscule nervous system. Light infestations actually help the grower as they are 'an easy alternative to flower thinning' (Blommers, 1994), but tend to build up after a few years and may require spraying, for example, with thiocyclam. But in a warm spring the flowers may open before the weevils can lay eggs, a further example of asynchrony between pest and plant (Section **5.2.1.4(g)**). The larvae develop in ~2–3 weeks. Miles (1923) records nine parasitic wasps in *Pimpla*, *Apanteles*, *Campolex*, *Meteorus* and *Habrocytus* from juveniles and an unidentified ichneumon from an adult. Surviving larvae pupate in the capped blossoms, emerging in late June. These adults feed on leaves of apple and other top fruits in July, and then take up winter quarters. When all development like this takes place within the confines of a capped flower the traces would provide good material for life table work (Section **11.4.2**), yielding valuable quantitative field data on the dynamics of this and, perhaps, similar species.

Anthonomus signatus attacks flowers in the Rosaceae including strawberries, and *Rubus* species such as blackberries, dewberries and raspberries. The female cuts off the flower in which she has oviposited, the larva developing in the fallen bud, a behaviour similar to that of some lamiine beetles (Section **4.2.1.2(e)**), and one preventing any further negative influence from the plant (Section **2.4.2**). Similar behaviour occurs in *A. musculus*, a pest of cranberries. *Anthonomus eugenii* attacks peppers.

6.2.1.2(d) COLEOPTERA; Curculionidae. *Anthonomus grandis*. Cotton boll weevil. A major, specific pest of cottons. This weevil has the distinction of being one of few insects immortalized in song. That the song's style is 'The Blues', invokes the depression it had on those to whom it fell to pick the damaged bolls. Another insect, a scarabaeid beetle (possibly *Geotrupes*), is immortalized in Grey's Elegy, also mournfully. While these beetles induce depression, the ancient Egyptians revered scarab beetles, *Scarabaeus sacer*, for their industry (Section **8.2.4**), while Thais keep jars of tenebrionid beetles in maize, symbolizing productivity. The boll weevil spread into the USA from Mexico as cotton plantations became more extensive. Starting in 1893 in south-west Texas, it had by 1922 spread throughout the Cotton Belt to North Carolina (Smith, 1998), a rate of some 80 km/annum. While much of this was due to the transport of unprocessed cotton, flying weevils have been caught at ~600 m, and exceptional flights can cover ~50 km/day. Although it is a key pest in only half of the Cotton Belt, it is reputed to be the most costly pest in American agriculture, totalling US$15 billion (Smith and Harris, 1994). A similar spread has also occurred in South America, while *A. vestitus* is already a cotton pest in Peru and Ecuador.

The adults, which are ~6 mm long, feed on the flower buds (squares) and seed pods (bolls) of wild and cultivated cotton, but also on the pollen of many plants, including grasses. They may breed on some other malvaceous plants, particularly *Hampea*, which may have been its original food, and also on *Cienfugosia*, *Hibiscus* and *Wissadula*. They generally lay eggs singly in the buds at a maximum rate of ~12/day, but more usually 4–7/day, similar to that in *Apion dichroum* (Freeman, 1967a). Their achieved fecundity (AF) is 100–300. Cotton bolls eventually disintegrate as a result of larval feeding although, as in *A. pomorum*, pupation occurs within them. Losses can amount to ~8% of the crop, which is of course *a much greater percentage of the profit margin*. Unlike the many univoltine weevils of flowers and seeds, there are from two to seven annual generations according to ambient temperature and humidity (Smith and Harris, 1994). This is partly due to the extended period of flowering and fruiting in cotton and is a contributory cause of the high incidence of attack, especially in late season. Under favourable conditions generation length is <30 days. Like clover seed and apple blossom weevils, adults overwinter under litter in protected places, hibernating preferentially within ~50 m of the field edges (Fye *et al.*, 1959). Estimated survival during winter varies greatly, probably having a considerable influence on the severity of attack in the next season (Smith and Harris, 1994), as envisaged in Andrewartha and Birch's (1954) theory of population (Section **11.2.2.3**). Adults also sometimes diapause in spring and autumn and may live 2 or even 3 years, the old ladies having lower oviposition rates.

Since 1980 the boll weevil has been eradicated or greatly reduced in numbers over much of the Cotton Belt. Pheromone traps are used to monitor population size. Then, if necessary, weevils are variously destroyed (Smith, 1998): (i) using their aggregation pheromone to trap them; (ii) using SMT; (iii) growing short-season cotton and the judicious use of planting dates; and/or (iv) by destroying overwintering sites, especially those in crop waste (Section **13.3.2.3**). Insecticides are applied only when needed. Apart from the environmental benefits, US$1 spent in the area-wide eradication programme has accrued ~ US$12 in return. You should make such an investment!

Today, harvested cotton is baled in large, wrapped modules for transport to the factory, where lint is separated from the seed (ginning). Adults may thus be transported many kilometres and escape if the air temperature is above the flight threshold of ~20°C (Sappington *et al.*, 2006). Escapees naturally compromise the eradication programme. Temperature varies within the module, affecting dispersal. Virtually all weevils are killed in the gin. Although *Bracon mellitor* and *Triaspis curculionis* (Braconidae), *Eurytoma gossypii* (Eurytomidae) in the USA, and *Catolaccus grandis* (Pteromalidae) in Central America attack this weevil, little has been done on biocontrol (Matthews, 1989). *Heterospilus megalopus* was introduced from southern Mexico, but has a far lower rate of oviposition than *A. grandis* (Morales-Ramos and Cate, 1993). In Nicaragua, a between-season trap crop of cotton has been effective. Control methods are detailed by Smith and Harris (1994).

6.2.1.2(e) LEPIDOPTERA; Glyphipterygidae. *Gliphipteryx cramerella*. Cock's foot moth. A specific, temperate pest of cock's foot grass. Cock's foot grass, *Dactylis glomerata*, is important in pasture improvement. Among other species, rye grasses, *Lolium* spp., are used in this way. Cattle and sheep are selective grazers and after a time distasteful species tend to build up in fields by natural selection. Reseeding with the preferred grass species is therefore necessary. Hence, the culture of such grasses for seed is an economic undertaking.

The minute brown and gold moths fly in sunshine in June and July, females depositing several eggs per flower head. These hatch quickly and the larvae destroy the flowers and reduce set seed. After feeding they bore into the stem where they overwinter. When fields are cut for seed and fodder, a low cut removes more larvae, so reducing a carry-over population to the next year. While *D. glomerata* is a common hedgerow species, in which scattered populations of the moth exist, their flight is weak, so that control in the field is critical. Natural control is apparently achieved by several small hymenopteran parasitoids. Apart from its pest status, the species would be another good subject for population regulation studies as it probably has limited dispersal and trace methods (Section **11.4.2**) can be used for much of the life cycle.

6.2.1.2(f) LEPIDOPTERA; Pyralidae. *Maruca testulalis*. Maruca or mung moth or legume pod borer. A broad-spectrum, pantropical pest. It attacks various peas and beans worldwide and also groundnuts, castor, tobacco and rice. It is a fairly large pyralid moth with a wingspan of 16–27 mm. It has dark brown forewings and diagnostic white hindwings with a dark marginal border. Eggs are laid on flowers, or occasionally on pods, and caterpillars eat them, the seeds and even the leaves. When mature they are ~15 mm long, whitish with a dorsal row of dark spots. In legumes, pupation is regularly in the pod. In Kenya, cowpea varieties with long peduncles and divergent pods show resistance to this moth (Okeyo-Owuor and Oloo, 1991). *Crotalaria* spp. have been suggested as a trap crop (Hokkanen, 1991; Section **13.2.3.5(c)**). *Maruca vitrata* attacks cowpeas and beans in African savannahs (Abate *et al*., 2000). *Homoeosoma electellum* eats the flowers and seeds of sunflowers in California, Texas and across the southern plains of the USA. Transgenic plants expressing *Bt* endotoxins have a potential for the control of these moths.

6.2.1.2(g) LEPIDOPTERA; Gelechiidae. *Pectinophora* (= *Platyedra*) *gossypiella*. Pink bollworm. A pantropical and warm-temperate pest of cotton. Confined south of 38°N and to the Malvaceae. This smallish (wingspan 15–20 mm), mousy brown moth with indistinct darker blotches probably originated in India (Matthews, 1989), or perhaps the New Guinea region, found its way to Egypt in 1906 and to Mexico in shipments of cotton seed in 1911 (Johnson, 1969). It then spread to southern USA (1917) and to parts of the Caribbean and South America (Gutierrez *et al*., 1986). There are fears that it could spread to south-eastern US states (Venette and Hutchison, 1999) although higher rainfall there may prevent this. Individuals can fly ~100 km and have been captured at a height of ~1000 m. It is potentially a most serious pest of cotton, despite the strong yield compensation of this crop. It may cause great destruction, not only damaging the lint but also reducing the yield of cotton seed oil, while the bored bolls may rot. It affects okra and a few *Hibiscus* spp. (Section **13.3.2.3**), which provide alternative food when cotton is unavailable (Section **13.1.2.2**). Even so, moths may emerge from diapause too early when larval food is scarce, a further case of *phenological asynchrony*.

Adults overwinter in the north of its distribution but breed continuously in the tropics, where its generation length is ~1 month. According to availability, eggs are laid either in flowers or bolls, but unlike *Heliothis* (Section **6.2.1.2(g)**), the AF is only 100–200. Eggs are at first white, becoming red prior to hatching. Larvae develop their distinctive pink colour in the later instars. Larval diapause may occur under short day conditions when temperatures are falling (Gutierrez *et al*., 1986), even under sub-tropical conditions. As in codling moths pupation sites are various, either in the seed or in debris under the plants, a strategy which reduces the population density of the pupae (Section **10.2.1**), in turn lowering natural mortality from enemies. Also the emergence period is long (1–2 months), so spreading risk (Section **9.7**). Destruction of crop residues is an effective control of the inactive stages. This is feasible for annual crops grown in flat fields and would be effective for coffee berry borers on mountain coffee, but the steep, often rocky nature of the terrain and the fact that the crop is perennial make such measures impractical. The moth also overwinters in seed waste where cotton is processed initially. *Collops* spp. (Coleoptera, Malachiidae) and ladybirds such as *Hippodamia convergens* consume the eggs.

Insecticides kill adults and eggs but the larvae are protected within the bolls. In California, the SMT (Section **13.2.2.1**) has been used. This method requires easy mass rearing of the pest, sterilization, and flooding the wild population with treated insects, which is hence driven to extinction. But the moth's strongly migratory capability, rather as in *Plutella*, tends to confound the method. Records exist of its penetrating, on southerly winds, Texas from Mexico (Johnson, 1969). Nubile females from the cotton canopy call males using a sexual pheromone. Synthetic pheromones (Section **13.2.3.5(d)**) catch and/or confuse ardent males (Witzgall *et al*., 2008), in train decreasing the proportion of fertilized eggs. This method is successful in that it may reduce necessary insecticidal application by 80%, in a crop where such chemicals are often used lavishly (Section **13.3.2.3**). Destruction of plant residues and strict observance of a closed season for the crop are also effective. Transgenic cottons expressing *Bt* toxins (Carrière *et al*., 2001) impact the moth in that emergence from diapause is far lower than normal. But despite all these tactics the species remains a serious pest.

Pectinophora japonica, which originated in eastern Asia, has been found in the eastern USA, while *P. scutigera* is confined to Queensland, Australia, and New Guinea. *Keiferia lycopersicella* is another gelechiid pest. It attacks tomatoes in northern Mexico and California, USA (Trumble *et al*., 1994).

6.2.1.2(h) LEPIDOPTERA; Noctuidae. *Heliothis* (= *Helicoverpa*) spp. Cotton bollworms, corn earworms, tomato fruit worms. Tropical to warm-temperate, broad-spectrum and highly mobile pests. There are some 80 species of this genus, but only four are major pests, a facet of commonness and rarity covered in Section **9.4**. In the New World, *H. zea* and *H. virescens* cause >US$1 billion damage annually, maintaining huge, shifting populations between 40°N and 40°S. *Heliothis armigera* is widely distributed in the Old World, including Australasia, where it has formed a sub-species, while a fourth species, the highly migratory *H. punctigera*, is endemic to Australia itself (Fitt, 1989). Apart from cotton, maize and sorghum, crops from diverse families such as Papilionaceae (peas, lucerne), Compositae (sunflowers) and Solanaceae (potatoes, tomatoes) are attacked. In Australia alone, *H. armigera* and *H. punctigera* have together been recorded from 161 plant species in 49 families. Like many noctuid moths, they are truly polyphagous and if crops are absent there are other plants in legions on which they can maintain their numbers. This effect is often important in allowing a spring generation to build-up numbers before the crops themselves are underway. However, conditions in central Australia may allow breeding of *Heliothis* spp. after autumn and winter rains, especially on diverse Compositae and Papilionaceae in the Lake Eyre Basin. Such moths migrate massively to crop-growing eastern areas in spring (Gregg *et al*., in Drake and Gatehouse, 1995). The fertile corner of Western Australia also suffers, with *Heliothis*, undeterred by fences erected to exclude plagues of emus and wallabies, often arriving in huge numbers. Studies using genetic markers, blocks of sequential alleles called *microsatellites* that characterize specific populations (Scott *et al*., 2005), show that migrant *H. armigera* are surprisingly variable genetically, both between regions and years. This extends work by Gould *et al*. (1980), who found that regional variation in cannibalistic tendencies in *H. virescens* had a genetic basis. But *H. zea*, apart from its predilection for cannibalism, also attacks *H. virescens* and probably many other caterpillars that it may encounter.

Mean AF in all species is high (~1000), indeed, some females lay up to 3000 eggs. Both fecundity and fertility are strongly influenced by food quality and, for example, are greater on maize than on cotton. Typically, eggs are laid close to buds or flowers. The small caterpillars feed on these structures, but are prone to disperse among the plants, while the later instars bore pods or fruits and on cotton, the bolls, but usually keep part of their bodies outside their food. They also consume leaves. They pupate in the soil. *Heliothis* spp. are generally univoltine in high latitudes but have up to five generations in the tropics.

Heliothis has a series of facultative diapause strategies by which its species can endure cool weather in low-latitude, temperate winters and dry summers in many regions. In the USA, the incidence of winter diapause increases with increasing latitude. In North Carolina (35°N) both *H. zea* and *H. virescens* larvae respond to reducing photoperiods of ~12 hours and reducing temperatures of ~20°C by entering diapause after pupating. But not all pupae diapause in such conditions, resulting in a considerable variation in emergence times in spring, thereby spreading risk (Section **9.7**). And for diapause in *H. zea* at least, different genetic strains exist. Summer diapause, allowing moths to endure long, hot dry periods, occurs in *H. fletcheri* in the Sudan in the November to June dry season. A drop in soil temperature, associated with the rains, breaks this resistant stage, rather as wetting does in the eggs of some grasshoppers. A similar diapause, initiated by high temperature, exists in *H. virescens* in Arizona and California, and might well occur in *H. punctigera* in central Australia.

There are three flight behaviours: (i) trivial, appetitive movement within the canopy of the food plants; (ii) medium-range movement within the boundary layer (Section **10.2.4.5**), extending a few kilometres; and (iii) long-distance nocturnal migration above the boundary layer, extending hundreds of kilometres (Fitt, 1989; Feng *et al*., 2005). In the Middle

East and parts of North Africa, *H. armigera* attacks early crops such as chickpeas in April, and cotton in June. It is strongly migratory, spreading from North Africa to many parts of Europe on south-easterly winds. In China, spring rainfall suppresses its populations materially (Wu and Guo, 2005). In the USA, there are spring migrations of *H. zea* and *H. virescens* to the Gulf and Delta States from maize-growing areas in northern Mexico. Migrant moths have been taken farther north in light traps before local populations emerge. SMT has been investigated in *H. virescens* and *H. zea*, but although irradiated males mate (Carpenter *et al*., 1989), the highly migratory habit of these moths probably makes the method impractical.

In the Americas, *H. zea* and *H. virescens* have between them >60 recorded species of hymenopteran and dipteran parasitoids. Several *Trichogramma* species, such as *T. pretiosum, T. minutum* and *T. exiguum*, and the scelionid wasp *Telenomus heliothidis* attack the eggs. The braconid wasps *Apanteles marginiventris*, *Cotesia kazak, Cardiochiles nigriceps*, *Microplitis croceipes* and *M. demolitor* and the ichneumons *Campoletis sonorensis* and *Hyposoter* spp. attack larvae. The tachinid flies *Eucelatoria bryani, E. rubentis* and *Archytas marmoratus* are common larval and pupal parasitoids, the former genus laying eggs directly on the late larvae and the latter producing planidia (Section **8.2.2.5**(**h**)). On some resistant tomato varieties with dense trichomes on the leaves, these planidia become entangled and hence become unintended victims (Kennedy, 2003). In India, there are 77 recorded parasitoids of *H. armigera* (see Tripathi and Singh, 1991). *Heliothis zea* but not *H. virescens* can encapsulate *Cardiochiles* larvae (King and Coleman, 1989). The coccinellid beetle *Hippodamia*, nabidid bugs, green lacewings such as *Chrysopa*, the wasp *Polistes* and a variety of spiders are predators. But even this battery of enemies often fails to restrain populations of *Heliothis* since their *en masse* immigration and high AF lead to inverse density-dependence (Section **11.4.4.2**).

Insecticidal control of *Heliothis* should be most effective when eggs are being laid or larvae are small. In the past huge quantities of traditional insecticides were used on cotton since it is grown extensively and not human food. Indeed, as in *Plutella* and *Nilaparvata*, the major pest status of *Heliothis* is a result of the overuse of insecticides. Insurance spraying (Section **13.3.1**) takes no account of the great natural mortality due to predators, which may do a better job without cost. On Oklahoma, USA, cotton, natural mortality of the eggs and first two larval instars of *H. virescens* was >99% (Young and Wilson, 1984, in King and Coleman, 1989). With the probable decrease in the effectiveness of insecticides, integrated pest management (IPM, Section **13.3**) emphasizes that the role of predators must be enhanced and possibly supplemented by repeated releases of parasitoids. The minute wasps *Trichogramma* spp. have been used with some successes in various cotton-growing regions. But the cost of producing them is high, as they are needed at a density of over a million/ha. Various microbial preparations may be applied, particularly *Bt* and the fungus *Nomuraea rileyi* (Section **13.2.4.5**). GM cotton expressing *Bt* toxin is being used increasingly. In India, trials with genetically modified cotton expressing the gene *Cry1Ac* have a fairly high resistance to bollworms (Qaim and Zilberman, 2003), and also increased yields. Transgenic cottons are being used increasingly in China (Wu and Guo, 2005; Section **13.3.2.3**) and require less spraying.

Several other moths attack cotton. *Diparopsis watersi* extends across the sub-Sahara from Yemen to Senegal, and is virtually confined to cotton. *Earias vittella* is an important pest of cotton in India. Other budmoths in this genus, which is multivoltine and lacks diapause, include *E. biplaga* in Africa, *E. huegli* in Australia, and *E. cupreoviridis* in China and other parts of South-East Asia. *Earias insulana* is widely distributed in the Old World. Their food plants are mainly in the Malvaceae. Larvae of the Neotropical migrant *Alabama argillacea*, whose adults are peculiar in being able to pierce some fruits, may eat early crop cotton leaves in the Gulf States and later the squares and bolls. Control should be attempted only after >50% defoliation, using *Bt* or trichlorfon, in order to avoid killing *Heliothis's* parasitoids (Matthews, 1989). The larvae also eat wild Malvaceae. The larvae of the hairstreak butterfly *Strymon molinus* occasionally bore cotton squares.

6.2.1.2(i) LEPIDOPTERA; Tortricidae. *Endopiza viteana*. Grape berry moth. A pest east of the Rockies. Moths emerge from the soil when vines are flowering and lay eggs on the stems, flower clusters or young berries. Larvae feed on the last two structures, leaving a mass of silken webbing. First-generation larvae pupate in a folded, semi-circular section of the leaf. Some 2 weeks later, second-generation females lay their eggs on the developing grapes, into which their larvae bore. These larvae also pupate in folded leaf sections, which may fall to the ground later. Eggs are often parasitized by *Trichogramma minutum*. Specific methods of soil tillage around the grape trellises kill many of the fallen pupae (Davidson and Lyon, 1986). These authors also give spraying techniques. Another tortrix moth, *Cochylis hospes*, attacks sunflowers grown for oil production.

6.2.1.2(j) DIPTERA; Cecidomyiidae. *Contarinia* spp. Cereal midges. Temperate pests of cereal and grass flowers. Some other midges infesting grain and fruit. Stem *Contarinia* (Section **4.4.4(a)**), have short adult life spans and pupate in the soil. Wheat blossom midges are similar but oviposit in newly opened flowers. They are potentially more serious, since after they have consumed pollen and other floral structures grain cannot develop: the marketable product is destroyed. It is important, therefore, not to let pupal numbers build up when wheat is being grown continuously. In this case, deep ploughing (expensive because of extra fuel costs) in autumn to bury the pupae, and a soil treatment before seed drilling, may be necessary. Alternatively, in an emergency, fogging on a still evening when the midges are mating and ovipositing, as is often done for tropical mosquitoes, could reduce crop losses. Direct application of an insecticide at this time using a boom sprayer is unlikely to be cost effective. Since adult midges have such short lives and daily cohorts of adults emerge, several applications would have to be made. A more environmentally friendly and effective strategy is to switch to a break crop such as oilseed rape or ley.

Contarinia sorghicola, although probably originating in southern Asia, now attacks sorghums (*Sorghum vulgare* and *S. bicolor*) worldwide. AF is low (~25 eggs/female), and initially several eggs are laid on the ovary of a single flower, resulting in up to ten larvae. Unlike most *Contarinia*, this midge pupates within the plant spikelets, and outside the tropics larvae in cocoons often pass the winter in this location. Larval and pupal survival are density dependent (Lampo, 1994; Section **10.2.3.7**). Adults live only 1–2 days, while under favourable weather the life cycle may be <3 weeks, allowing a devastating build-up that may prohibit growing sorghums locally. In the tropics, up to 18 annual generations can occur. The eggs may be parasitized by *Tetrastichus venustus*. In addition, the eulophid parasitoid *Aprostocetus diplosidis* has some value for biocontrol, its rate of attack being density dependent within seed heads. Parasitism by the eupelmid wasp *Eupelmus popa* has been recorded both in Asia and the Americas. Since the midge overwinters in the spikelets, their remnants should be ploughed under in autumn. But it has alternative food in wild sorghums, such as *S. halepense* (Johnson grass) and *S. arundinaceum*, from which it may spread to crops (Section **13.1.2.2**).

Sitodiplosis mosellana, the orange wheat midge, affects wheat flowers in parts of Europe and central Canada. Here, larval competition for resources in the wheat spike can greatly reduce the size of adult females and consequently their AF (4–105 eggs) (Smith and Lamb, 2004). Biocontrol, using *Macroglenes penetrans* (Pteromalidae), had not been very successful, but some improvement has occurred with the introduction of *Platygaster tuberosula* (Platygasteridae) (Olfert *et al*., 2003). These wasps together destroy up to 60% of the eggs. Another grain midge, *Orselia oryzivora*, attacks rice in parts of Africa. *Contarinia pyrivora* lays eggs in European pear flowers, the gregarious larvae infesting the fruits, which become deformed and later decay. Mature larvae overwinter in silken cocoons in the ground, but pupate in spring, a common general sequence. Other such midges are *C. ribis* on gooseberries, *C. rubicola* on blackberries and *C. viticola* on vines.

6.2.1.2(k) DIPTERA; Cecidomyiidae. *Dasineura oxycoccana*. Blueberry gall midge. An emergent pest of blueberries, cranberries and related cultivations. Some other *Dasineura* pests. Many fruit crops are in the Rosaceae. But blueberries, cranberries and the like are in *Vaccinium*, relatives of heather in the Ericaceae. This midge became important recently in the USA, and also in the Mediterranean, with increasing cultivation of these fruits. In Florida, USA, failure of the former crop, 'rabbit-eye' blueberries, reached 80% in 2004 compared to 15% in 1983 (Dernisky *et al*., 2005). Adults emerge here from the soil in February, with several generations ovipositing on the flower buds until flowering ceases in June. They also oviposit in leaf buds if flower buds are absent. In Mississippi, USA, *Aprostocetus* (= *Tetrastichus* sp.) (Eulophidae) is an effective larval parasitoid, and *Quadrastichus* is also found (Sampson *et al*., 2002). *Aphanogmus* spp. and *Ceraphron pallidiventris* (Proctotrupidae) also parasitize them, while larval *Toxomerus marginatus* and *T. geminatus* (Syrphidae) prey on them. Using these enemies for IPM has yet to be worked out, but breeding resistant crop varieties is underway. Incorporation of alleles from the wild *V. darrowi* into northern highbush blueberries produces a new cultivar (southern highbush blueberry) whose buds are resistant to this midge. But because of its early emergence, spraying with malathion and/or spinosad is necessary initially. *Dasineura ribis*, which is common in Northern Europe, oviposits in black currant flower buds, ultimately reducing fruit set.

Dasineura brassicae, the brassica pod midge, has also become more common with increasing cultivation of oilseed rape. Larvae damage the seeds and reduce oil yield. The wasp *Platygaster subuliformis* oviposits in its host's eggs, but the wasp's eggs do not hatch until the host is about to pupate (Williams *et al*., 2007). These authors show clearly what has been long suspected, that such wasps (and also *Phradis interstitialis* and *Tersilochus obscurator*) use anemotaxis (Section **10.2.4.3**) to locate their hosts. *Omphale clypealis* (Eulophidae) is another of its parasitoids. *Prolasioptera berlesiana* oviposits in developing olives, especially those already attacked by *Bactrocera oleae* (Section **6.3.1.1(o)**), inoculating them with the fungus *Spheropsis dalmatica*, on which the larvae feed. The fruits become black and drop to the ground wherein the midges pupate.

6.2.2 Sucking pests

Thrips form a distinctive order of sucking exopterygotes showing some affinity to the Hemiptera. While the extinct pollen-feeding Lophioneuridae date from the Lower Permian, and may represent the origin of this order, the first obvious thrip, *Karatothrips*, is from the late Jurassic. Thrips rarely exceed 2–3 mm, and bear a superficial resemblance to diminutive staphylinid beetles. Their wings, however, have a characteristic structure, with a rod-like central axis bearing long marginal setae. This strange design is found only in truly minute insects, such as mymarid wasps and ptilinid beetles, a striking case of convergent evolution. In some thrips, however, one or both sexes are wingless. The mouthparts are peculiarly asymmetrical but otherwise show a likeness to those of homopteroids. The large majority feed on living plant tissue, using their stylets to feed selectively from sub-epidermal cells (Ullman *et al*., 1992a, in Nault, 1997). But they have only a single feeding channel. First they inject saliva and then suck up the products. Pest thrips usually attack a variety of flowers, sucking the pollen, and are hence dealt with here, but thrips in general also affect other plant tissues. Some species kill small insects such as aphids. Most pests are in the sub-order Terrebrantia, in which the females have an ovipositor and lay eggs in plant tissue. In the Tubulifera this organ is absent, most species feeding on spores or being predatory. AF is often <50 eggs/female. The last two nymphal instars are generally quiescent, with the external wing pads becoming progressively longer. They recall the pupal stage of the Endopterygota, although this does not indicate affinity with this group (Richards and Davies, 1988).

They are primitively associated with fungi in dead wood (Hamilton, 1996; Normark, 2003), always haplodiploid and often colonial and parthenogenetic. In some species, males are unknown or rare. Despite their small size, some little predators, for example the anthocorid bugs *Orius laevigatus* (Venzon *et al*., 2002) and *O. insidiosus*, eat them. Several thrips transmit viruses, either Ilarviruses from pollen or Tospoviruses from leaves (Nault, 1997). Tospoviruses are acquired only by first instar nymphs and inoculated by the resulting adults.

6.2.2.1(a) THYSANOPTERA; Thripidae. *Thrips tabaci*. Onion thrips. This light brown insect is a pest of onions and other bulbs, cabbages, tobacco, beans, cotton seedlings and other crop plants. It may discolour the skins of table grapes. It affects all parts of the plant and transmits Spotted Wilt Virus of tomatoes (Ossiannilsson, 1966) and Iris Yellow Spot Virus of onions. It attacks leeks in Europe and late season cabbages in North America, moving in from adjacent crops of cereals, lucerne and clover as they are harvested (Shelton and North, 1986). Recently, its numbers have been suppressed by multiple treatments of imidacloprid and acetamiprid. This is expensive, but several other insecticides are ineffective. Resistant plant varieties can be used but may not have good properties for marketing. But on onions straw mulches suppress its numbers and may be used as a trap crop to lure this little beast from cotton seedlings.

6.2.2.1(b) THYSANOPTERA; Thripidae. *Thrips imaginis*. Plague thrips. Davidson and Andrewartha (1948) famously studied the numbers of this species in rose flowers in relation to weather. But *T. imaginis* are widely important in Australia as pests of apples where they may reduce the crop by up to 75%. They feed, however, on the pollen of a variety of flowers, this being essential both for egg production and for nymphal development. Because pollen grains vary in size so much, the individual feeding time per grain varies from a few seconds to over half a minute (Kirk, 1987), but under optimal conditions >1000 grains may be destroyed per thrip per day. *Thrips imaginis* also sucks the sap from other floral structures. The last two nymphal instars pass ~1 week in leaf litter, before producing winged adults that search for flowers. Their numbers within any flower is a function of the density of suitable flowers in extended habitats, be they apple orchards or rose gardens, a good example of a bottom-up effect (Sections **9.8** and **12.3.1**). *Thrips meridionalis* affects flowers of the Rosaceae, but especially nectarines and peaches. Damage to the stamens reduces fruit set while damage to the ovaries results in necrotic patches on the fruitlets, later causing distortion (Alford, 2007).

6.2.2.1(c) THYSANOPTERA; Thripidae. *Kakothrips nemorum*. Pea thrips. This thrip attacks flowering peas, subsequently resulting in twisting and silvering of the pods. Naturally this is more significant in cultivars such as *mange tout* in which the pod itself is human food.

6.2.2.1(d) THYSANOPTERA; Thripidae. *Taeniothrips inconsequens*. Pear thrips. This mainly parthenogenetic thrip affects the leaves, flowers and fruit of pears, plums and cherries, where it also oviposits. Nymphs start to enter the flower buds in May where they damage petals, stamens and styles alike, which results in russeting and distortion of the fruit. It is univoltine, the juveniles complete development in early summer and drop to the soil, where they remain dormant until 'pupation' in October.

6.2.2.1(e) THYSANOPTERA; Thripidae. *Heliothrips haemorhoidialis*. Greenhouse thrips. This originally tropical species attacks several greenhouse crops, but is found outside in Mediterranean regions. It is spanandrous and parthenogenetic and, atypically, 'pupates' on the food plant.

6.2.2.1(f) THYSANOPTERA; Thripidae. *Limothrips cerealium, L. denticornis.* Corn thrips. These blackish species, which are associated with cereals, are highly migratory and capable of sustained flight. The former is found in Europe, southern Australia, New Zealand and the USA. *Limothrips denticornis* breeds in grass and cereal leaf sheaths, where brothers mate their sisters before the latter emigrate (Hamilton, 1996). *Anaphothrips striatus* breeds in grasses but may cause sterility in oat spikelets.

6.2.2.1(g) THYSANOPTERA; Thripidae. *Frankliniella occidentalis*. Western flower thrips, and some related species. This is a widespread and polyphagous pest of glasshouse crops. Like some earwigs it is a true omnivore and may prey on mite eggs. It may be carried long distances by wind and can be spread internationally in packaging, having arrived in Europe in the 1980s. It reproduces sexually and parthenogenetically at temperatures >10°C, taking only 12 days to develop at 30°C. Apart from direct damage to leaves, flowers and fruits, it may carry Tomato Spotted Wilt Virus, an organism that also affects cucumbers (Gaum *et al*., 1994). UV-reflective mulches reduce the thrips' ability to locate such plants. Potted petunias are especially attractive to this species, providing convenient traps. In India, *F. sulphurea,* and in Trinidad, *F. insularis*, impair the yield of pigeon peas (*Cajanus cajan*, also called dhal). *Frankliniella tritici,* the grain thrip, is a small, yellow and orange pest that is widely distributed and abundant in North America. It affects grass and cereal flowers, resulting in less seed or grain production. Among other crops it also attacks strawberries, causing misshapen fruits, as do *F. intonsa, Thrips fuscipennis* and *T. major*. *Anaphothrips obscurus* is another common species associated with cereals in this region (Shelton and North, 1986).

6.2.2.1(h) THYSANOPTERA; Thripidae. *Scirtothrips aurantii* and *S. citri*. Citrus thrips. These are tropical or sub-tropical species affecting citrus flower buds, new flushes and fruit, which becomes scarred and distorted. *Scirtothrips citri* has been a major pest of Californian citrus for over a century, but by the 1980s traditional insecticides began to fail, while some residues actually increased its AF (Morse and Zareh, 1991). Biocontrol with the predatory mite *Euseius tularensis* has also been attempted. *Liothrips oleae* is found abundantly throughout the Mediterranean Basin. The adults overwinter under the bark of olive trees. It commonly has three annual generations, attacks all parts of the tree and results in loss of yield.

6.3 Pests of Fruits and Seeds

6.3.1 Biting pests

These can be divided into two distinct groups: (i) outdoor pests in fields, orchards and occasionally in forests; and (ii) indoor pests of products stored in barns and silos or being transported in vehicles and ships. For a well-illustrated and comprehensive review of fruit pests, see Alford (2007).

6.3.1.1 Field and orchard pests

6.3.1.1(a) COLEOPTERA; Byturidae. *Byturus tomentosus*. Raspberry beetle. A specific, temperate pest of *Rubus* fruits (raspberry, blackberry and loganberry, Rosaceae). The wild relatives of the above crops are conspicuous members of the gap phase of seral development in broad-leaved temperate woodlands. These phases last only a few years so that *Byturus* must continually find new sources of food. So, one expects them to be pre-adapted to locate new cultivations of these crops. This is a clear example of how synecology can augment autecology. Adults are yellowish-brown, 3–4 mm long and overwinter in the soil. They feed in summer on flowers of wild Rosaceae until the *Rubus* berries develop in July and August. Then females oviposit on the surface of the young fruits. As the berries ripen the larvae tunnel into the 'plug', and hence become concealed. Pupation is in an earthen cell. *Byturus rubi* and *B. bakeri* are North American. As with all small fruits to be tinned, only very low levels of infestation can be tolerated.

6.3.1.1(b) COLEOPTERA; Scolytidae. *Hypothenemus hampei*. Coffee berry borer, in Brazil, broca do café. A specific and most important, pantropical pest of coffee. *Hypothenemus* is a bark beetle genus that has radiated into micro-environments other than the original type, since several of them have evolved to attack fruits and seeds. Even so, some species such as *H. burmanus, H. dimorphus* and *H. pusillus* infest tree seedlings in nurseries (Nair, 2007). In many ways, the biology of *H. hampei* recapitulates its under-bark origins (Section **4.2.1.2(g)**). Indeed, if berries are scarce they may breed in coffee branches, often entering at a fork (Winston Shaw, personal communication).

In Jamaica, *Coffea arabica* flowers several times early in the year, so the berries that form later are in various stages of development. Females gain access to a green berry via the apex, making a short tunnel, and remain there for some time. This behaviour is typical of other tropical, seed-eating beetles, and may prevent the plant from excising its young infected offspring (Janzen, 1981). But in Neotropical coffee, during summer small avian insectivores and several ant genera eat these females. Survivors bore into the berries in the mature green stage, just before they turn yellow. Several egg batches are laid, 8–12 at a time, so the larvae hatch progressively (Freeman, unpublished data). In all, ~80 eggs may be laid. A bluish fungus is associated with the larvae and species of *Fusarium*, *Penicillium*, *Candida* and yeasts have been described, but their role in beetle nutrition is equivocal. No advantage was found for three species of these genera (Pérez *et al*., 2005). Larvae destroy one of the beans and then pupate in the berry, which turns dark brown. Rarely, the mother penetrates the second bean. This may be because the plant effectively marshals its defences into the attacked fruit (Section **2.4.2**). Even so, other females may bore the same berry later, and losses of up to 85% have been reported.

The brown berries, which either remain on the bush or fall to the ground and wherein the new generation of adults passes the winter, are a major source of infestation for the next fruiting, but many females emigrate from the natal site. The sex ratio is strongly spanandrous, with only ~10% of the brown, non-dispersive males, as would be expected from Hamilton's work (Section **8.2.2.5(o)**). This has the population consequence of effectively increasing fecundity. But in addition, the male-killing attentions of *Wolbachia* (Vega *et al*., 2002; Section **10.2.3.9**) have been described from several countries. Males are much smaller than females, being 1.6 mm compared to 2.5 mm in length. Sib-mating occurs before the females disperse. Many females probably reach distant reproductive resources and so any plantation is at risk of attack by a proportion of fertile immigrants.

Control is more effective when integrated (Jaramillo *et al*., 2006). Obviously, clean husbandry is called for. The removal of brown berries from both bushes and the ground and the destruction of the overwintering beetles in them are ideal, but in practice hard to achieve because of poor labour (who in the main do not appreciate the importance of their job) and/or difficult terrain, often on rough and rocky mountain slopes. Mansingh (personal communication, 1992) has shown in Jamaica that spraying the fallen berries is ineffective, which exemplifies the protection that a plant structure may confer upon an insect pest. Further work to develop an effective IPM strategy is continuing. Spraying the green berries with the cyclodiene endosulfan has often been used in Jamaican coffee, but fortunately is being phased out, as this and an alternative, the organophosphate chlorpyrifos, are persistent and toxic to mammals. Endosulfan washes down into streams where it builds up in freshwater shrimps (*Macrobrachium* and *Atyia*), a traditional tasty treat for Jamaican villagers.

Before the pest's arrival in the 1970s, little care of the bushes was needed apart from fertilizing and pruning. But its rapid spread and the fact that the females have rather long wings suggest that it has good powers of migration, and hence nation-wide control is essential. More recently, pheromone traps have been used successfully, and the possibility of using entomopathogenic nematodes has been investigated. Winston Shaw, a local coffee farmer in Jamaica, tells me that perfectly good traps can be made at minimal cost by boring holes in the necks of plastic soda bottles (see Fig. 13.5). These, suitably baited with a methanol/ethanol mixture, can be deployed at a high density. But if traps are placed on a particular bush most of the suitable fruits on that bush are attacked too. It is better to place them peripherally or on bananas grown as an intercrop. Donald Clark, who has a smaller operation, tells me that since he stopped spraying, losses from borers have been minor. Farmers have also found that providing water for migrant warblers in the dry season attracts these little insectivores into the plantations. It is clearly possible to combine a pheromone trap with a water dispenser. Reproduction also occurs at the processing factory, which becomes another focus of population.

Preparations of the fungus *Beauveria*, sprayed at the green berry stage, trap females who have made initial borings. Other candidates for control include the well-known nematodes *Steinernema feltiae* and *Heterorhabditis bacteriophora*. The eulophid endoparasitoid, *Phymastichus coffea*, originally described from Togo, parasitizes females as they wait to penetrate the berry (cf. *Microctonus*, Section **6.2.1.2(b)**). In Colombia, up to 85% parasitism is recorded, confirming its potential as a biocontrol agent (Jaramillo *et al*., 2006). In some areas, the bethylid wasps *Prorops nasuta*, *Cephalonomia stephanoderis* and *C. hyalinipennis* attack the broods in the berry, being attracted to the beetle's frass, but they may prove to be less useful than *Phymastichus*. The control potential of the braconid wasp *Heterospilus coffeicola* is also being investigated. Damon (2000) and Jaramillo *et al*. (2006) give reviews and bibliographies. The extraordinary *Hypothenemus pubescens* breeds in grasses, while *H. obscurus* and *H. eruditis* are recorded from maize in Nigeria. Another scolytid beetle, *Hylastinus obscurus*, attacks clover roots.

6.3.1.1(c) COLEOPTERA; Scolytidae. *Conophthorus* spp. North American pine cone beetles distributed mainly along the Rocky Mountain range. This is another specialized scolytid genus, mainly attacking pine cones (Mattson, 1980a, b) with several species being distributed down the Rocky Mountains into Mexico. For example, *Conophthorus edulis* is found in pinyon pines, *C. ponderosae* in Ponderosa pines, *C. resinosae* red pines and *C. radiatae* in Monterey pines (Mattson, 1980a, Table 2). In all there are ~12 species. It seems likely that all of them can vector pitch canker, as *C. radiatae* is known to do (Storer *et al*., 2004). Mattson estimated that *C. resinosae* destroys ~80% of all the cones produced. This is a species whose numbers are limited *bottom-up* by its resources (Section **10.1**).

The young adults attack apical buds and then females bore into the base of a developing cone, generally severing its vascular supply, and lay several eggs. Thus, as in some lamiine beetles (Section **4.2.1.2(e)**) the plant is unable to respond to the beetle's attack, for example, by resin flow. Egg numbers relate to cone size, but each female attacks several cones. The cones become infested with larvae, destroying the seeds. Cone production is curtailed in many pines. Enemy insects are few, although a bethylid wasp, *Cephalonomia utahensis*, parasitizes *C. radiatae*. In *C. resinosae*, desiccation and over-heating are probably the major cause of the >85% juvenile mortality (Mattson, 1980a). The severity of attack is influenced not only by variation in the size of the pest's population, but also by weather and the widely fluctuating number of cones set by trees in different years. This illustrates an important generality in the population ecology of some other flower and seed pests. The number of cones on a tree equals the carrying capacity (*K*) of the patch. While in early models (Section **11.5.2**) *K* was regarded as a constant, this example reminds us that it may vary widely (see Dempster and Pollard, 1981). A highly variable annual production of seed by perennial plants may be an evolutionary adaptation against seed loss due to a specialist seed eater. In years of great seed abundance the pest can consume only a small fraction of them. A similar form of seed production occurs in beech (*Fagus*).

6.3.1.1(d) COLEOPTERA; Curculionidae. *Conotrachelus nenuphar*. The plum curculio. A mainly central and eastern North American pest of apples, peaches, plums, cherries and blueberries. After overwintering outside or inside orchards in sheltered places, the adults ascend the trees during flowering and feed and mate on their leaves. A female makes an incision in the developing fruit, lays an egg and then, as in *Apion*, pushes it into the cavity with her rostrum. Then she makes a crescent-shaped cut near to the first incision. These traces provide a ready means to identify the presence of the pest. Both feeding by adults and their reproductive efforts damage the fruit. According to Comstock (1940), plum trees but not cherry trees excise the infected fruit but in either case the mature larvae pupate in the soil. Various estimates of AF are ~50–70. Reservoir populations of this weevil occur in wild *Prunus americana*. Parasitism of the eggs is reported in some areas and in plum fruits gummy exudates may kill them. Larval parasitism by the wasps *Aliolus curculionis, A. rufus* and *Tersilochus conotracheli* occurs at low levels (generally <5%) (Armstrong, 1958; Mampe and Neunzig, 1967), but I found no mention of parasitoids of the adults. Armstrong records *A. curculionis* emerging from a host larva and then *both* pupating. This weevil is univoltine in the north (Michigan) and bivoltine in the south (the Carolinas) of its distribution.

High levels of spraying with organophosphates (azinphos-methyl, phosmet) and pyrethroids (permethrin, esfenvalerate) are still used in many orchards to provide commercial levels of control. But 'greener' methods include the use of kaolin (Section **13.2.3.5(f)**) and various traps baited, for example, with benzaldehyde and the aggregation pheromone grandisoic acid (Leskey and Wright, 2004). The related weevil *Craponius inaequalis* attacks grapes.

6.3.1.1(e) COLEOPTERA; Curculionidae, Rhynchitinae. *Neocoenorrhinus* (*Caenorhinus*) *aequatus*. Apple fruit weevil. A temperate pest of top fruits, widely distributed in Europe. This weevil is 3–5 mm long, black, with chestnut elytra and a prominent, curved rostrum. It bores the fruitlets of wild trees, often species related to the cultivar fruits, so housing most of its population. But it also attacks top fruits such as apples, pears and plums, eating holes for nutrition and oviposition, and so is similar to *Apion*, *Anthonomus* and many other weevils. Damage occurs just after fruit set, from late May to early July. Many small holes are made in the fruitlet, which is often excised. The larvae bore the fruit and pupate in the soil emerging in late summer. As in *Apion*, much of the population exists outside the crop and there is a migration to woodland leaf litter to overwinter. *Neocoenorrhinus pauxillus*, found mainly in continental Europe, confines its depredations to leaves; but *N. cribripennis* bores olive fruits and *N. germanicus* those of strawberries and various *Rubus* spp. *Rhynchites auratus* and *R. baccus* are similar European species.

6.3.1.1(f) COLEOPTERA; Curculionidae. *Ceutorhynchus obstrictus* (= *assimilis*). Cabbage seed pod weevils. Holarctic pests of brassica pods, especially rape (canola), presently emerging in Canada. Again, these weevils have some behavioural and ecological similarities to *Apion* (Section **6.2.1.2(b)**). They are univoltine pests of brassicaceous seed pods when these are big enough to permit larval development. And they overwinter in woodlands, especially under trees that give extra protection from low temperature (Ulmer and Dosdall, 2006). Their diapause requires a cold period of at least 16 weeks before it can be broken (Cárcamo *et al.*, 2009). They leave their winter quarters in spring when temperatures reach ~15°C, males tending to leave before females. In Canada, they feed on the flowers of cruciferous weeds before flying to crops such as rape and Oriental mustard. In Europe, where rape is sown in late summer, they fly to the crop directly. The gonads develop during this initial feeding. Then, the females oviposit in the developing pods. The larvae destroy the seeds, bore out when mature and pupate in the soil, development lasting 1–2 months. Again, as in *Apion*, the new generation continues to feed on the crop building up fat stores before flying to overwintering sites.

Many parasitoids are associated with this weevil both in Europe (32 species) and North America (24 species). The pteromalid wasps *Stenomalina gracilis, Trichomalus perfectus* and *Mesopolobus morys* are ectoparasitic on the larvae within the pod. The last two have potential as biocontrol agents (Mason *et al.*, 2011). Several other pteromalid species are associated with this pest, while *Microctonus melanopus* (Braconidae) afflicts the adults. Synthetic pyrethroids, such as deltamethrin (Section **13.2.3.2**), presently give a measure of economic control.

6.3.1.1(g) COLEOPTERA; Curculionidae. *Curculio spp*. Nut weevils. *Curculio* contains species with an advanced structure, their fine, elongated rostra being capable of boring small holes in nuts. As in *Apion*, the females bore into the larval food, inserting an egg through the hole. *Curculio neocorylus* and *C. nucum* (**Fig. 6.1**) attack hazelnuts and *C. caryatrypes* and *C. sayi* chestnuts.

6.3.1.1(h) HYMENOPTERA; Symphyta. *Hoplocampa testudinea* (apples), *H. brevis,* (pears), *H. flava* and *H. minuta* (plums), *H. cookei* (cherries). Fruit sawflies. Eurasian and North American pests of specific top fruits in the Rosaceae. As in many other sawflies, these species are specific to a given crop plant. Their eggs are inserted into the sides of the receptacles (Graf *et al.*, 2002), cultivars with white flowers being particularly attractive to them. Temperatures >7°C are needed for development. The young larvae bore the surface of fruit, later they bore deeply and leave tell-tale traces of frass at the entrance. Depending on the relative ages of the fruit and pest, a larva attacks one, two or more fruits, but multiple attack is more common in *H. flava*. *Hoplocampa testudinea* invaded New York State, USA, from Europe in 1939, presumably in infected apples, and a year later was found in British Columbia, Canada. The ichneumon *Lathrolestes ensator* was introduced to control it. Another ichneumon, *Aptesis nigrocincta*, also attacks it and it is susceptible to fungi. Pupation is within the soil. Although non-selective insecticides are still used sometimes, *Quassia* extracts have been employed in organic orchards. *Pachynematus pumilio* is a specific pest of black currants in Northern Europe.

6.3.1.1(i) LEPIDOPTERA; Tortricoidea; Tortricidae (= Eucosmidae, = Olethreutidae). *Cydia pomonella* (= *Enarmonia*, = *Laspeyresia,* = *Carpocapsa*). Codling moths. Cosmopolitan pests of apples, pears, plums, apricots and some other fruits, more recently of walnuts. This economically important moth from a large genus has been classified over the years in a wide variety of generic and familial names. It is of special ecological interest because of the diverse ways it is redistributed. But there are other ecological comparisons that can be made with *Psila rosae* (Section **3.2.2.1(h)**). Both are pests of originally widely scattered plants that have been cultivated and monocultured. Both attack the marketable product and can be dispersed with it. Apart from having reservoir populations in crab apples, these moths may be found in pears, peaches, sweet chestnuts and walnuts. *Cydia splendana* is a more specific pest of these nuts.

Cydia pomonella (**Fig. 6.2**) reached North America from Europe about 1800 and Australia somewhat later. With few exceptions it occurs wherever apples are grown. The adults, with a wingspan of ~18 mm, have greyish dappled forewings with a distinctive dark brown blotch near the apical margin. They should not be confused with the similarly patterned *Epiblema uddmanniana,* the bramble shoot moth (see Fig. 660 in Alford, 2007). There is a genetically based dispersive polymorphism: some adults are restricted to a 60 m ambit while others move several kilometres (Keil *et al.*, 2001). Even so, there can be significant genetic variation between populations. This work should be linked to studies on the *Pgi* locus in other Lepidoptera (Haag *et al.*, 2005; Section **10.2.4.1**). Females lay only 30–50 eggs and, under north temperate conditions, often place them in July and August on apple leaves or in the eye of the developing

Fig. 6.1. *Curculio nucum* (Curculionidae). It shows the extreme specialization for boring of the head and mouthparts. Source: Wikimedia Commons, credit to Mathias Krumbholz.

Fig. 6.2. The notorious codling moth, *Cydia pomonella* (Tortricidae), a cosmopolitan pest of apples. Source: Wikimedia Commons, author Olei.

fruit. But wherever eggs are laid, the close presence of a fruit is necessary to evoke oviposition. Indeed, in California, USA, they have laid eggs directly on stored apples. In south-west England, Glen (1975) found 48–75% egg mortality from Heteroptera and Dermaptera. Near Stockholm, Sweden, predation on the eggs approached 50% (Subinprasert and Svensson, 1988), but this might have been atypical because their experimental material was glued to the apple leaves. Predators were ladybirds, earwigs and the bugs *Anthocoris* and *Blepharidopterus*. Eggs on fruitlets had lower rates of predation, but these eggs were lost more often when the fruits were naturally excised. *Trichogramma* spp. often parasitize the eggs. Usually a single larva makes its way into the centre of the fruit where, as it matures, it may consume the developing seeds. But great mortality of first instar larvae occurs, often due to predation by mites, lacewings and the various bugs. When two or more larvae are in a fruit they become cannibals if they meet, even though there is plenty of food. This is straight cannibalism not resource competition (Section **10.1.2**).

At harvest in early autumn, larvae bore out of the side or top of the fruit and crawl down the tree in search of places to diapause. In contrast to their cannibalistic behaviour in fruits, these larvae emit an aggregation pheromone from the cocoon, resulting in closer spacing of emerging adults and perhaps facilitating mating (Jumean *et al*., 2004). Such congregation contrasts with the usual dispersive behaviour of most mature lepidopteran larvae, and is also found in sawflies such as *Perga* (Section **5.2.1.3(f)**). But this pheromone can also attract *Mastrus ridibundus* (Ichneumonidae), which parasitizes them at this stage. Flaky bark on trees provides more overwintering sites (Solomon *et al*., 1976). Even so, intraspecific competition for these refuges may ensue. In warm parts of Europe, *Cryptus sexannulatus* and *Ephialtes caudatus* (Ichneumonidae) parasitize the pupae. The ectoparasitic eulophid wasp, *Hyssopus pallidus*, which is attracted to apple, enters larval borings or finds codling larvae under bark and lays batches of 10–30 eggs on or near them (Hausmann *et al*., 2005). This wasp employs two different searching behaviours, the progeny being strongly spanandrous (Hamilton, 1967).

In mild regions, *Cydia* may be partially bivoltine. Only some larvae diapause in the summer, the rest pass through to be reproductive adults, thus spreading risk (Section **9.7**). However, reducing photoperiods often induces larval diapause. Up to three annual generations occur in warm conditions. Trees may excise >40% of infected apples. Mature larvae then leave the fruit on the ground. Indeed, hibernation sites are diverse, leading to multiple ecological and economic outcomes. The tough hibernaculum may be spun under bark on a limb or trunk or on the ground under debris. In some cultivars the apple may be picked before the larva has left. If entry has been made through the eye this is hard to detect. Then, escaping larvae may spin up in boxes in packing sheds, in wholesale and retail markets, or in the purchaser's home, so reducing avian predation. Surviving larvae pupate in spring. Hence, passive movement within the marketable product leads to widespread redistribution, although mortality is very high in most natural situations (Solomon *et al*., 1976). These authors found that predation on trees by titmice caused ~95% mortality. Providing nest boxes for these birds in organic orchards would limit resident populations of this moth severely, and most likely several other pest insects, especially leaf rollers. Probably very few moths find suitable food plants if they leave apples purchased in cities.

Control of apple pests is not an operation that can be done piecemeal for one pest at a time. It must be integrated to combat all those pests that affect a given locality, cultivar and agronomic practice (see Section **13.3.3.2**). While insecticides may be used to disrupt oviposition, care must be taken in their choice and timing to minimize bad effects on beneficial predators. A spring treatment fenoxycarb (Section **13.3.3.2**) kills the over-wintered pupae, so reducing population growth in warmer climates (Blommers, 1994). SMT, pheromone traps (Witzgall *et al*., 2008), the nematode *Neoaplectana carpocapsae*, *Bt* and Granuloviruses (Jacques *et al*., 1994) have been used to reduce attack in several countries. Pheromone traps can assess changes in population accurately, improve timing of spraying and in train reduce costs and pollution. In British Columbia, Canada, re-invasion from other areas is a constant problem (Myers *et al*., 1998a and b) and reservoir populations had to be eliminated. Walnuts exported from California are regularly fumigated with methyl bromide. The unseen destruction of the fruit, however, is not the end of the damage. Bored apples may become mouldy in storage, and the resulting 'brown rot', caused by the fungus *Sclerotinia fructigena*, spreads throughout a whole consignment, another case of the multiplicative effect noted earlier. Hence, only a low infestation of the fruits is permissible.

6.3.1.1(j) LEPIDOPTERA; Tortricidae. *Cydia* (= *Grapholitha*) *molesta*. Oriental fruit moths. A widespread pest of many top fruits. Some other species of *Cydia* and similar pests. These moths are found in Japan, where they replace *C. pomonella*, in China, India, Australasia, the Mediterranean region, South Africa, the USA and South America as far south as Chile. Early in the year they operate as stem borers, and later generations (four to five per year) attack fruits when available, especially peaches. As in *C. pomonella*, diapausing larvae overwinter in a hibernaculum and pupate in spring. *Macrocentrus ancylivorus* (Braconidae) is used for biocontrol on peaches in the USA, but it is effective only on early generations in the twigs. It has alternative hosts in caterpillars on weeds. As in codling moths, *Hyssopus pallidus* may lay batches of eggs on the larvae. Synthetic pheromones are used to disrupt mating in these moths (Witzgall *et al*., 2008).

Cydia (= *Grapholitha*) *funebrana* is the plum fruit moth, *Grapholitha* (= *Cydia*) *prunivora* attacks *Prunus* species and also pome fruits, while *C. pyrivora* is a more specific European pest of pears. All such fruits for export are best held at ~2°C for several weeks (Neven, 2004). *Cydia coniferana* larvae live in silk-lined tunnels under the bark of *Pinus, Picea* and *Abies*, where they feed on the cambium, while *C. strobilella* oviposit on the seed cones of a variety of North American spruces (*Picea* spp.). *Grapholitha interstinctana* is the clover head caterpillar. *Lobesia botrana* attacks European vines, the first generation affecting the flower buds while the second destroys maturing grapes. Reservoir populations (Section **13.1.2.2**) exist on *Berberis*, *Hedera*, *Ligustrum* and *Lonicera*. The larvae of the tortrix *Cryptophlebia ombrodelta* bore litchi fruit, while locally *Cr. leucotreta* can be a serious pest of cotton bolls and citrus in sub-Saharan Africa from Burkina Faso to Uganda.

6.3.1.1(k) LEPIDOPTERA; Tortricidae. *Cydia nigricana*. Pea moth. There is a natural reservoir of the moth in wild vetches in hedgerows. Adults emerge in early summer from such sources or from old pea fields and are particularly common in eastern England. Females lay eggs in batches of twos and threes all over the plants. The wandering young larvae eat some leaf and flower tissue before boring into the pods. Here, varieties that can be planted early show resistance because the pods are too tough at the time of the attack (cf. winter moth) and late-sown varieties are also attacked less. Mature larvae drop to the ground, burrow deeply and overwinter in a hibernaculum, coming near to the soil surface to pupate in spring, an interesting strategy. Deep burrowing promotes better protection from low winter temperatures, which can be severe in open fields. But were they to pupate at this depth emerging adults would have difficulty in escaping from the soil (cf. lepidopteran pests of stems, Section **4.2.1.2**). In processing peas for tinning, cooking kills the larvae, which float to the top of the vat and are skimmed off. Occasionally a larva is saved for a longer posterity in a tinny tomb, awaiting discovery by a distraught housewife. Deep cultivation of the soil in winter kills larvae in their hibernaculae, while summer foliar sprays kill eggs and wandering larvae, and probably deter ovipositing adults. Moth populations can be monitored by using the attractant (E, E)-8,10-dodecadienyl acetate, preferably by generating elongated odour plumes from triangular traps (Lewis and Macaulay, 1976).

6.3.1.1(l) DIPTERA; Cyclorrhapha; Tephritidae (=Tripetidae). In the Diptera a number of mainly tropical or sub-tropical flies attack fruits. Most of the important ones belong to the Tephritidae (Bateman, 1972), which contains the Trypetinae, the Ceratitinae and the Dacinae. Females bear an ovipositor, males have broad, patterned wings which they wave in species-specific sexual displays. There are *generalist species* that attack a series of pulpy fruits. These are long-lived, mobile, fecund, and lack diapause. Then there are *specialist species* that feed on specific fruits. These synchronize their life cycles with that of their food and have a long diapause in the soil (Aluja and Mangan, 2008). Evidence is accumulating that many of these flies (e.g. *Zonosemata*, *Toxotrypana*, some *Anastrepha*), although relatively small, make daily migrations between the crop and sheltered habitats where they spend the night (Aluja, 1996). Note that some *Drosophila*, that are even smaller, can move at least 1 km in an hour (Coyne *et al*., 1982; Section **12.1**).

6.3.1.1(m) DIPTERA; CYCLORRHAPHA; Tephritidae. *Rhagoletis pomonella*. Apple maggot. A pest of North American apples, other top fruits in the Rosaceae and hawthorns (haws).

Rhagoletis spp. are Nearctic, numerous, generally univoltine and oligophagous. Adult *R. pomonella* are a bit smaller than house flies (**Fig. 6.3**), mainly black with yellow head and legs, and have distinctive, white transverse abdominal bands. They often feed on honeydew deposited by homopteroids and employ a bacterial symbiont, *Pseudomonas melophthora*, which synthesizes amino acids. While they fed originally on hawthorns, a new strain developed about 1860 in the Hudson Valley on imported apples. In 1960 a race specific to cherries was found in Wisconsin, USA. Two distinct races probably *formed sympatrically* on hawthorn and apple (Bush, 1969; Smith 1988; Section **9.10**), which may well have been caused by *phenological asynchrony*. While an estimated 6% of genetic interchange exists in one experimental population in Michigan, USA, separation is maintained because the patterns of diapause in the two races are adapted to the different temperature regimes in the two food plants (Filchak *et al*., 2000), and strongly maladapted on the 'wrong' plant. Females do not oviposit in native crab apples, possibly because they ripen late. Mating often occurs on developing fruits, which are male territories and this too assists racial separation. Flies detect fruits by size, shape and reflectance (Boller and Prokopy, 1976); indeed, sticky dark-red spheres, 8 cm in diameter, are effective for their entrapment. Females insert single eggs into fruit, marking its surface with an oviposition deterring pheromone (ODP; Section **10.2.5.2**). AF is <150 in orchards, >300 in the laboratory. The larvae bore throughout the fruit so destroying it, and drop to the ground to pupate. Although mortality is often low in the fruit, the overwintering puparia are killed by crickets, ants and carabid beetles, especially so as some spend several winters in the soil. Such risk spreading (Section **9.7**) also occurs in *Perga affinis* and *Neodiprion sertifer* (**5.2.1.3(f)**).

Fig. 6.3. The North American fruit fly *Rhagoletis pomonella* (Tephritidae). Source: Wikimedia Commons, author Joseph Berger.

Rhagoletis spp. support a rich fauna of largely braconid parasitoids. These wasps are egg parasitoids (*Utetes canaliculatus*, *U. richmondi* and *U. lectoides*), or afflict the larvae (*Opius*, *Utetes*, *Diachasmimorpha*, *Aphaereta auripes* and *Diachasma alloeum*) (Forbes *et al*., 2010). Many of them attack other *Rhagoletis* spp. Larvae in hawthorns, and presumably in *Cotoneaster*, suffer higher parasitism from *Diachasmimorpha* (= *Opius*) *mellea*, whose ovipositor can reach them more easily in the smaller fruits (Porter, 1928, in Price *et al*., 1980). These parasitoids probably use the host's ODP as a cue to locate their victims, as is known for *O. lectus*. The diapriid wasp *Coptera pomonellae* is a pupal parasitoid.

In North America, the suavis species group (*R. suavis, R. completa, R. juglandis, R. boycei and R. zoqui*) infests walnuts, while *R. mendax*, of the pomonella group, favours blueberries (Bush, 1969), *R. zephyria* snow berries, *R. cornivora* dogwood, *R. basiola* rose hips, and *R. indifferens* and *R. cingulata* cherries. In the high and dry climate of the Mexican Plateau (Sierra Madre), the last-named fly has evolved several sub-species (Rull *et al*., 2011). It also occurs in Europe. In South America, *R. lycopersella* is multivoltine on tomatoes in arid subtropical regions. In Europe, *R. cerasi* is widespread on cherries.

6.3.1.1(n) DIPTERA; CYCLORRHAPHA; Tephritidae, Ceratitinae. *Ceratitis capitata*. Mediterranean fruit fly. A largely tropical, very broad-spectrum pest of fruits. This widespread and destructive pest is found throughout tropical and Mediterranean regions. Unlike most *Rhagoletis* species, it attacks a diversity of crops: citrus, mangoes, peaches, pome fruits, figs, kiwi fruits, guavas and coffee. The ovipositor penetrates the fruit and batches of 8–12 eggs are laid. A single female may deposit up to 600 eggs distributed over dozens of fruits. Females also feed at the punctures. Eventually, if not picked, the fruit falls and the surviving larvae pupate in the soil. However, in common with many other Diptera and Lepidoptera, the mature larvae disperse before pupating, so lowering their density. In cooler regions it overwinters in the pupal or adult stages but cannot survive most European winters. The life cycle takes between 3 weeks and 3 months according to temperature, so in warm climates population increase can be very rapid.

Females may also scar fruit with the ovipositor, thus reducing its quality, but lay no eggs. Since they are attracted to sweet solutions (and to decomposing fruit), they may be controlled by spraying trichlorphon or malathion and sugar solution in large droplets on the foliage. Eradication programmes in California and Florida in the USA have been successful for a time, but costly. One in the former state in the early 1980s cost over US$100 million. In Hawaii, USA, and in the Canary Islands SMT has been used successfully to eradicate this pest, but outside islands such programmes have been compromised by immigration. And there is the ever-present danger of re-introduction in fruit smuggled in from other tropical countries. Ignorance in action is a pernicious process.

Zonosemata electa, which attacks peppers and aubergines in eastern North America, emerges from the soil in early summer, and lays eggs on the fruit for at least a month (Boucher *et al*., 2003). The flies move daily between the crop and woodlands and thickets (see Section **6.3.1.1**(**k**)), which makes perimeter trap cropping (Section **13.2.4.4**) an efficient and 'green' method of control.

6.3.1.1(o) DIPTERA; CYCLORRHAPHA; Tephritidae, Trypetinae. *Anastrepha ludens, A. obliqua*, *A. fraterculus,* other *Anastrepha* (>190 spp.). Mainly polyphagous, Neotropical fruit flies. Despite a plethora of species, as in *Rhagoletis*, it is likely that many more cryptic ones (Walter, 2003) exist, since detailed studies on *A. fraterculus* s.l., using isozyme analysis, have revealed a large cryptic complex (Steck, 1991). In addition, three different wing banding patterns occur regionally. Other such complexes probably also occur (Norrbom and Korytkowski, 2009), while a single orchard may contain as many as 15 species. *Anastrepha* often oviposit in a wide variety of Neotropical fruits, being one of the region's most devastating pests (Aluja, 1994; Aluja and Mangan, 2008). They are widespread with several larvae developing in a single fruit, rendering it inedible. Along with *Ceratitis capitata*, *A. fraterculus* s.l. is a major pest of fruit in Brazil, especially citrus. The adults are long-lived (>1 year), multivoltine and highly fecund (>1200). Generalists (Section **6.3.1.1**(**k**)) such as *A. ludens* (Fig. 6.4) and *A. obliqua*, that move between a variety of fruits during the year, are also serious pests.

Fig. 6.4. Another notorious tephritid pest, the tropical fruit fly *Anastrepha ludens*. Several other *Anastrepha* spp. attack Neotropical fruits. Source: USDA Agricultural Research Service.

Conservatively, single females could each destroy >100 fruits, often belonging to several species. In Jamaica, wild ('common') mangoes are usually riddled with *Anastrepha* larvae; perhaps 1 fruit in 20 escapes.

By contrast, a few monophagous species, like *A. crebra*, have a phenology synchronized with their fruit food, diapausing when it is out of season. In sub-tropical regions the adults of some species pass the cool weather in loose, multi-specific groups sheltering in denser foliage such as that of citrus (Bateman, 1972). Structurally primitive *Anastrepha* feed on the fruits of sapodilla, naseberry and star apple (Sapotaceae) and may represent the origin of this rapidly evolving genus. Perhaps sympatric speciation in *Anastrepha*, as in *Rhagoletis*, has been frequent since different strains of a given species vary in their complex mating behaviours. Indeed, in *Bactrocera cucurbitae* pre-mating isolation in experiments can be achieved rapidly (Miyatake and Shimizu, 1999). But because taxonomy is based only on adult females and the juvenile stages are poorly known, it makes critical work on their population dynamics impossible.

Eggs are laid singly (*A. obliqua*) or in large clutches (*A. grandis*) into the epicarp or mesocarp. This is partly dependent on the size of the ripening fruit. There are three larval instars that feed on the pulp but occasionally on the seeds as well. As in other tephritid flies, the larval and adult guts are modified to accommodate symbiotic bacteria (*Enterobacter*, *Erwinia*, *Klebsiella*, *Microbacter*, *Pseudomonas*, *Proteus*). These may function to break down fruit tissue and its defences, synthesize amino acids and suppress pathogenic microbes. And as in *Drosophila*, the larvae often produce alcohol dehydrogenase as a means of surviving in over-ripe fruit. Pupation is usually in the soil, whose characteristics, such as moisture, compaction and pH, influence survival. In common with many other higher Diptera, a period of maturation is needed before adults become sexually active. Protein and other nutrients are required for gonadal development, and these are obtained not only from fruit but also from faeces. The few species that attack the seeds within the fruit have a brief period of maturation, however, presumably because these structures are a rich nutritional source.

Anastrepha has many enemies. Several species of indigenous braconid wasps (*Doryctobracon aeriolatus*, *D. brasiliensis*, *D. crawfordi*, *D. zeteki*, *Opius argentinus*, *O. hirtus, O. tucumanus*, *O. vierecki* and *Utetes anastrephae*) and the cynipid genera *Eucoila* and *Ganaspis* attack juvenile *Anastrepha*. The exotic braconid species *Diachasmimorpha longicaudata* and *Biosteres arisanus* are common. There is a significant correlation between the wasp's ovipositor length and the size of the fruit in which larval *Anastrepha* are parasitized (Fig. 6.5) (see Fig. 1 in Sivinski and Aluja, 2003). *Aganaspis pelleranoi* (Eucoilidae) is a broad-spectrum pupal parasitoid that also attacks *Ceratitis capitata* (Ovruski, 1995). *Fopius aristanus*, from Asia, is attracted to fruit volatiles that are induced when *Anastrepha* oviposits in them (Pérez *et al*., 2013). Staphylinid beetles and ever-present ants, such as *Solenolepis geminata*, are predators. Field studies in Chiapas, south Mexico, using *Heterorhabditis bacteriophora*, achieved a maximum kill of 74% of the larvae entering the soil (Toledo *et al*., 2006), with pupae being resistant. However, the densities of this nematode required are probably prohibitive commercially. The ascomycete fungus *Stigmatomyces aciurae* attacks the adults (Aluja, 1994). As in wireworms, bark beetles and some gall midges, excessive water can kill juveniles.

In most countries much of the fly population lives outside orchards, for example in common mangoes, guavas and star apples, so there is usually a huge reservoir of population (Section **13.1.2.2**) to attack commercial fruits. Despite their rather small size, migrations of >100 km have been reported. Both *A. ludens* and *A. obliqua* fly between adjacent habitats, rather in the manner of shuttling melolonthine beetles (Section **3.2.1.2**(**b**)).

Sprays of poisoned baits are used traditionally, despite their ineffectiveness and their potential to reduce parasitism. Then, soil under the trees can be sprayed, for example with diazinon. But as Aluja puts it bitterly: '*Anastrepha* control and management has … been conceptually and technically stagnant for the past 35 years'. McPhail traps (Southwood, 1978) used in monitoring are inefficient in that they retain only a small percentage of the female flies they attract. In Mexico, Peru and southern USA, SMT has been employed to combat *Anastrepha*. This should be an effective, intrusive technique, reaching flies throughout the reservoir population, especially in mobile species, but irradiated *A. ludens* males are far less successful as mates than wild flies (Moreno *et al*.,

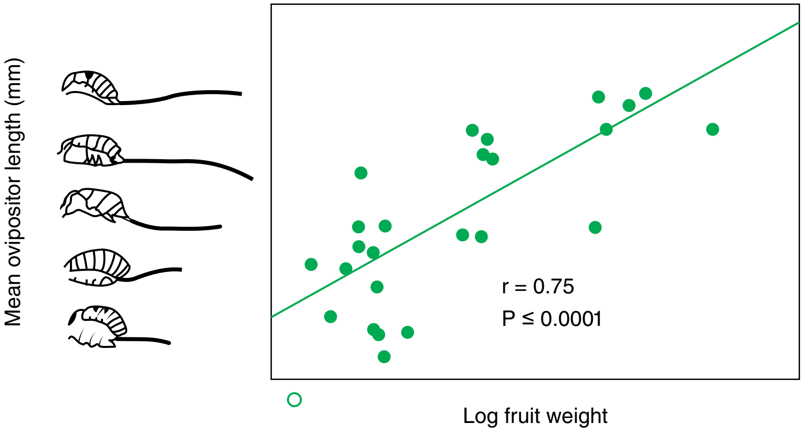

Fig. 6.5. Ovipositor lengths in parasitoid wasps in relation to fruit weight. From: Sivinski, J. and Aluja, M. (2003) The evolution of ovipositor length in the parasitic Hymenoptera and the search for predictability in biological control. *Florida Entomologist* 86, 143–150.

1991). Of course, biocontrol too is intrusive, but while two braconid species, *Dia. longicaudata* and *Dor. crawfordi*, have become established, their influence on *Anastrepha* populations is uncertain. Orange traps of various shapes are highly attractive to several species, however, and 20 cm spheres of this colour may act as a supra-normal stimulus (Eibl-Eibesfeldt, 1970), acting like a huge ripe fruit. Spheres with reflectance in the 600–650 nm range (orange) are also attractive to some tephritid flies (Section **6.3.1.1(p)**), as are red spheres for *Rhagoletis pomonella* (Section **6.3.1.1(m)**). *Anastrepha* also have a liking for human urine. Finally, potentially infected fruits for export must be treated either with hot water or refrigeration to kill young juveniles.

6.3.1.1(p) DIPTERA; CYCLORRHAPHA; Tephritidae, Dacinae. *Dacus* (= *Bactrocera*) spp. Old World fruit flies (>700 spp.). Dacine fruit flies in the Old World and Australasia are equivalent to *Anastrepha* (Section **6.3.1.1(o)**) in the New World, sharing many similarities with them. Most species attack fruits, but are strongly oligophagous or even monophagous. As in *Anastrepha*, the most serious pests are polyphagous and multivoltine. These include *Dacus dorsalis*, the Oriental fruit fly, *D. tryoni*, the Queensland fruit fly and *D. curcurbitae*, the melon fly (Fletcher, 1987) which affects Cucurbitaceae and tomatoes in Africa, India, South-East Asia and the USA. *Bactrocera oleae* is a monophagous scourge of Mediterranean olives, an ancient cultivar of the wild olive from the sub-Sahara. This fly is also present in South Africa, Central America and, from 1998, California, USA, and adjacent parts of Mexico (Daane and Johnson, 2010). At least seven *Bactrocera* spp. occur in South-East Asia.

In the main their life cycles are similar to those in *Anastrepha*. The females use their ovipositors to insert eggs in ripening fruit, wherein larval development through three instars takes place. Again, pupation is in the soil. At 25°C development of most species takes ~3 weeks. After emergence, adults require a period of several days to reach sexual maturity. They may live for at least 3 months, and those that enter reproductive diapause during hot, dry periods when fruits are unavailable live longer. Thus, the generations may overlap.

Like *Anastrepha*, complex relationships exist with diverse bacteria, *Enterobacter*, *Klebsiella*, *Pseudomonas* being common to both dacine genera. The pioneering work of Petri (1910, in Fletcher, 1987) showed that *P. savastanoi*, a pathogen of olives, is symbiotic with *B. oleae* (Hagen, 1966). In such flies diverse bacteria multiply in a special oesophageal bulb and are released in batches into the gut. Later, they congregate in rectal diverticula and infect the eggs prior to oviposition, namely vertical transmission (Section **7.3.2.4(b)**). Females also puke bacterial vomit onto the surface of fruit and oviposit through it. These symbionts are essential for larval growth, for if females or fruits are injected with an antibiotic the juveniles quickly die. Again as in *Anastrepha*, these bacteria may also detoxify plant defences, suppress other microbes and produce amino acids.

The physical environment has direct and indirect effects (Section **10.1**) on the numbers of dacine flies (Fletcher, 1987). Depending on temperature, *D. tryoni* and *D. dorsalis* may have three to eight generations annually, while *B. oleae* has three to six within the Mediterranean. But *B. minax*, which attacks citrus from Nepal to south-west China, is univoltine. The lower threshold for its development is 6–9°C, but this is again retarded at ~28°C and temperatures >30°C are lethal. Growth is also reduced under dry conditions and in unripe fruit. Competitive interactions often occur both within and between species, but evidence for an oviposition deterring hormone, known in *Rhagoletis*, is lacking. Hence, competition between larvae within the fruit may result. Once more, as in *Anastrepha*, a battery of mainly braconid parasitoids attack them, but in larger fruits they avoid the wasps by burrowing deeply. Since commercial fruits are usually large they provide a partial refuge (Section **9.9**), which may be a contributory reason for *Dacus*' pest status. In California, USA, *B. oleae* females spread defensive compounds from the fruit near the oviposition scar. These act to deter other females. Even so, several eggs are sometimes laid in one fruit, leading to local 'hot spots' of competition (Burrack *et al.*, 2009). Despite this, survival in the fruit is often >80%. However, in the soil mortality of the pupae is often much higher. Even so, in Corfu, there is high survival (>30%) to the adult stage (Kapatos and Fletcher, 1986). As in *Anastrepha*, poisoned baits laced with spinosad (Section **13.2.3.2**) and lures have been deployed to reduce populations of these pests. Synthetic sexual pheromones combined with ammonium bicarbonate are particularly attractive (Daane and Johnson, 2010).

Biocontrol using braconid parasitoids such as *Fopius arisanus*, *Utetes africanus* and *Bracon celer* is being researched. Both *Psyttalia humilis* and *P. lounsburyi*, brought from sub-Saharan Africa, have been released in California, the latter becoming established in coastal areas (Daane *et al.*, 2015). The physically harsher climate inland apparently limits their spread. The resident braconid wasp *P. kapaunae* may cause up to ~40% mortality locally. Again, some of these parasitoids of larvae have short ovipositors, insufficient to reach hosts deep in the fruit, especially in large olives. Therefore larval flies remain in a spatial refuge (Section **9.9**). So ovipositor length is an important feature when devising biocontrol with wasps (Sivinski and Aluja, 2003). Infected fruit becomes useless for canning and lowers the quality of olive oil. Annual losses total US$800 million.

From 1919 to 1974, the melon fly spread up the south-western islands (Nansei-shoto) of Japan towards Kyushu. After suppressing its populations with a male lure (methyl eugenol) and insecticides, SMT, in which up to 200 million flies/week were released, eradicated this pest progressively (1985–1993) down the island chain (Koyama *et al.*, 2004). Improved lures have been developed in Hawaii (Jang *et al.*, 2007) where this fly has been present for >100 years. The traditional attractant, cuelure, is less effective than the new raspberry ketone formate. But without stringent quarantine the melon fly could easily be spread widely in infected fruit.

6.3.1.2 Pests, mainly beetles, of grain, flour, dried fruit and other stored products

These pests have evolved from insects originally attacking field crops or their wild ancestors. Historically, when we began to store grain for example, these insects were harvested and became adapted to the conditions of grain stores. Several of them (*Rhyzopertha*, *Callosobruchus* and *Sitophilus*) are still found in the field and in stores. They all form *continuously breeding* populations under favourable hygrothermal conditions and comprise Coleoptera Polyphaga, (Dermestidae, Anobiidae, Tenebrionidae, Bruchidae and Curculionidae), and a few small moths (Phycitidae, Pyralidae and Gelechiidae). In moths, only the larvae feed on the product. In some beetles, the adults do not feed either and so are short lived. Lately, the cosmopolitan psocids *Lepinotus reticulatus* and *Liposcelis entomophila* have become an increasing problem in stored grain (Opit and Throne, 2008) while *Li. decolor* affects stores in South Australia. Other species are *Li. bostrychophila* and *Li. paeta*. Apart from movement with stored products, many *Liposcelis* spp. form part of the aerial plankton (Section **10.2.4.1**).

As in strike flies (Section **7.4.2.1**) and soil-forming insects (Section **8.2.4**), pests of stored products comprise primary species that come in initially and secondary ones that arrive later. Indeed, finer ecological divisions can be made. For primary pests attacking uninfected products, there are those that feed *externally* and those that feed *internally*. Of course, this is relevant only to products like grains, pulses or items sufficient to conceal an individual insect: there cannot be an external feeder in flour or meal. Larval internal feeders, such as *Sitotroga* and *Rhyzopertha*, bore into the grain as first instars, those of the weevils *Sitophilus* hatch there in bore-holes made by the extended mouthparts of their mothers. An individual larva of such pests completes its development in a single food item (Section **12.2.1**), the grain. The quantity and quality of food that the grain provides, largely determines the size of the adult and in turn its AF (Section **10.2.5.2**). There can be no such relationship for external feeders. These primary pests are important commercially for two reasons: (i) when they feed internally they may be difficult to detect; and (ii) their action greatly reduces the value of a formerly clean product.

Secondary insects attack only after the primary ones have done their dirty work. Some of them operate only after great degradation of the stored product has occurred. At such times microbes are abundant and the product is valueless. Another important factor is the potential rate of population increase of the pest under storage. Several pest beetles have been used in studies on population ecology because they provide simple experimental material. For example, they have been used to investigate the effects of temperature and moisture on fecundity and longevity (Section **10.2.5.1**). Unsurprisingly, these effects permit much higher rates of population increase in the tropics. They have also been used to investigate competition. Of course, such studies have little relevance to their original ecology in separate heads of grain in the field where redistribution can occur.

We can touch on only some of the problems involved in controlling pests of stored products. Much of the infestation that occurs is due to national and global transport of infected products or by *residual* stocks in ships and stores harbouring these pests. A transporting ship or truck is simply a temporary, mobile store. Efficient quarantine procedures and keeping empty stores clean goes a long way to controlling such insects as several of them have limited individual powers of searching and finding new resources. Because infected products have low commercial value, prevention is by far the best option. Even so, to defray costs, infected products are frequently used in animal foods. When this is the case, care should be taken not to transport pests in them.

The control of pests in and between commercial storage is a blend of human and insect ecology. There are four major factors: (i) making a store that is ventilated but insect proof; (ii) screening incoming new products for pests; (iii) cleaning and treating all storage sections between use; and (iv) ensuring that infestation does not occur during transport. Stored products, like the pests that attack them, may be primary, comprising produce from farms, and secondary, those that have undergone various processing. Much unidirectional transportation is involved. For example, farm to grain store, to seed merchant, to mill, to food processor, to wholesaler, to retailer and finally to consumer. Pests may gain access to products at any of these stages. Large silos, such as those at ports, may hold up to 1000 tonnes of product. At this size compaction, particularly of damp grain, may cause the build-up of rock-hard deposits, making cleaning a dirty, difficult, but lucrative process.

Current control methods still employ insecticides either directly, such as deltamethrin and pirimiphos-methyl, or as fumigants, particularly phosphine. One of the better modern control methods is to store the products in sealed silos in which the internal atmosphere has enhanced levels of carbon dioxide and nitrogen (controlled atmosphere storage) (Wang *et al*., 2000, in Boyer *et al*., 2012). These gases are obtained from cylinders available commercially. This method, also used to suppress codling moths in stored apples, has the advantage of not causing taint or insecticidal contamination to the product and, in the case of living grain, not affecting viability. But for grain the method has yet to gain popularity. Grain is often stored at ~15% moisture, but the surface layer may absorb atmospheric water. Blowing air from outside through the silos, taking advantage of warm and dry weather, is commonly used for moisture control. An original African village method is to store the grain with an admixture of fine sand, often above the fire in a hut. Both the smoke and the abrasive effects of the sand make insect life difficult. Recently Fields and Korunic (2000) found that an admixture of diatomaceous earth to stored barley may result in >99% reduction of some pest beetles. Juvenile hormone or moulting hormone mimics can be applied. In domestic situations, controls are unlikely to be used and hence, infestations in homes will always provide a source of these pests for commercial situations: they are small but numerous reservoir populations. This recalls the situation in which untended fruit trees in domestic gardens are a source of pests for commercial orchards (Section **13.1.2.2**). For recent reviews, see Rees (2004) and Boyer *et al*. (2012).

Primary pests: Internal feeders

6.3.1.2(a) COLEOPTERA; Bostrychidae. *Rhyzopertha dominica*. The lesser grain borer. A tropical and sub-tropical pest. The family contains many wood-boring pests (see Section **4.2.1.2(b)**). The family is related to the Anobiidae, which contains furniture and tobacco beetles. The adults, which are less than 3mm long, attack both pre- and post-harvest grains and also milled rice, cereals and cassava. Their small size and their wood-boring capability make them difficult to exclude. Lacking an elongated rostrum like weevils, this and the following species lay their eggs externally on the stored product, the young larvae boring into it. Occasionally after an initial attack, some of the larvae of later generations will feed externally, so that this is not always an internal pest. The pupae too may be found internally or externally. Optimum conditions are ~34°C and 70% relative humidity (RH), when development takes ~3 weeks. The adults live up to 4 months; females deposit 200–400 eggs according to the type of food and the physical environment. Among other parasitic Hymenoptera, *Anisopteromalus calandrae*, a pteromalid wasp that attacks several other beetles in stored products, parasitizes the larvae. Another bostrychid beetle, *Prostephanus truncatus*, is common in the Neotropics, and now in Africa, and attacks field and stored maize, as well as other stored products. It is possible that the predatory histerid beetle *Teretriosoma nigrescens* could be used as a biocontrol agent.

6.3.1.2(b) COLEOPTERA; Chrysomeloidea; Bruchidae. *Callosobruchus maculatus*. Bean beetles. Pantropical pests specific to large grains and pulses. Bruchid larvae are often specific to leguminous seeds (Southgate, 1979), some genera being confined to a few plant genera apart from those transported by commerce. New and Old World species are separate. In the latter region, *Careydon* spp. affect many leguminous and other trees. Single seeds support single larvae. Leguminous trees are diverse in warmer climates and so are their bruchid pests. *Callosobruchus maculatus*, however, attacks beans in the field, stored pulses and maize, a selection that may relate to grain size. This must be newly evolved, since this pest originated in Africa but maize is New World. *Spermophagus* spp. attack *Convolvulus*, okra seeds and other *Hibiscus* spp. In *C. maculatus,* the eggs are glued to the bean's surface and larvae bore through the base of the chorion into the seed. In culture, Utida (in Nicholson, 1958, p. 113) showed that at high densities of *C. chinensis* AF is reduced and eggs are destroyed by other adults. The life cycle lasts ~3–4 weeks and AF is 80–100 under ideal conditions of 32°C and 90% RH. They pupate in the seed. Trichogrammatid wasps often parasitize the eggs. In West Africa the ectoparasitic wasp *Eupelmus orientalis* attacks the juvenile stages (Doury and Rojas-Rousse, 1994) in fields of cowpeas. There is a complex interaction (Section **11.5.2.3**) between *C. maculatus*, another common beetle *Bruchidius atrolineatus*, and several parasitoids, including *Uscana lariophaga* (Trichogrammatidae) in the eggs, and *Dinarmus basalis* (Pteromalidae) and *E. vuilleti* (Eupelmidae) in other juvenile stages. But under storage, *E. vuilleti* rapidly becomes the major parasitoid.

Adult *C. maculatus* do not feed and rarely live more than 12 days. They have a dispersive polymorphism, and workers such as Utida (1972) have described a strongly marked form that is more active in this respect, but has lower AF. Even so, their dispersive capability is poor with an effective radius of only 1 km. Thus, infestation in storage usually arises from contamination by juveniles, which are entirely hidden in the seeds.

Many other species of *Callosobruchus* occur, often being specific to particular regions. For example, *C. analis* and *C. chinensis* are originally Asian, but the latter is now pantropical. *C. subinnotatus* is West African and *C. theobromae* found in West Africa and India, while *C. rhodesianus* and *Zabrotes subafsciatus* are further pests. *Caryedon* is specific to seeds of leguminous trees such as *Acacia*, *Cassia, Bauhinia* and *Tamarindus*. *Bruchus pisorum* is found in field peas, but its larvae do not attack the stored product. They may, however, survive the winter as pupae within the pea and be planted out in spring, thus disseminating the population.

6.3.1.2(c) COLEOPTERA; Bruchidae. *Acanthoscelides obtectus*. This is a similar beetle of South American origin, where some 300 other species belonging to this genus are found. It is presently confined to the Americas and Africa. It attacks various dried beans (*Phaseolus* spp.) and there may be six or more generations in a year. The optimum conditions are 30°C and 70% RH. It is capable of reproduction at temperatures down to 18°C, however, and is often a pest in tropical highlands. The anthribid beetle *Araecerus fasciculatus* attacks coffee beans in storage.

6.3.1.2(d) COLEOPTERA; Curculionidae. *Sitophilus oryzae* (= *Calandra oryzae,* = *C. sasakii*). Rice weevils. Primary, cosmopolitan pests of grain. This important pest attacks rice, maize and other grain both in the field and in store. Its fine mouthparts permit it to penetrate the hardest grain, a feature probably allowing its primary attack. Typical of many weevils, the female chews a fine oviposition tunnel, deposits the egg and seals the tunnel with a secretion. The larvae destroy the kernel of the grain, rendering it valueless, and pupate within it. Optimum conditions are 27°C and 70% RH at which AF is 100–150 and development takes ~35 days, but at lower temperatures as many as 100 days are required. The duration of development is also influenced by grain quality. Adults may live up to a year. No reproduction is possible below 15°C. This species and the closely related *S. zeamais* are capable fliers, unlike the flightless S. *granarius* (Section **6.3.1.2**(**e**)), in which the metathoracic wings are vestigial.

6.3.1.2(e) COLEOPTERA; Curculionidae. *Sitophilus granarius* (= *Calandra granaria*). Granary weevils. Both this and the preceding weevil infested Roman grain stores (Osbourne, 1977, in Coope, 1979), but this species has a more northern distribution than *S. oryzae* and has greater resistance to low temperature. Adults are flightless. AF is 200–250 and maxima are achieved at lower temperatures than *S. oryzae*. The minimum for development is 11°C. They feed on a wide variety of grains, including wheat and barley, but are confined to stores. Staining a sample of the grain in acid fuchsin for a few minutes may reveal the presence of either species. After washing off the excess, the egg plugs show as bright red pin pricks.

6.3.1.2(f) LEPIDOPTERA; Gelechiidae. *Sitotroga cerealella*. Angoumois grain moths. Angoumois is a region of France to the west of Limoges, from

Fig. 6.6. The Angoumois grain moth *Sitotroga cerealella* (Gelechiidae), whose larvae bore into stored grain. Source: Wikimedia Commons, CSIRO.

which this little moth was originally described. The yellowish-white adult females (Fig. 6.6) have a wingspan of ~16 mm. Their wings are narrow and the hind ones bear long fringes, characters distinguishing them from any other stored product moth. They oviposit on the outside of the grain and the first larval instars bore in, leaving only microscopic traces of their entry. The larvae feed within a single grain and pupate immediately below its surface, leaving a little window for the adult to escape. The species is normally transported with infected grain. Not only bulk grain may be implicated, however, it may also be transported in bird seed and even in corn ears used for decoration.

Primary pests: External feeders

6.3.1.2(g) COLEOPTERA; Dermestidae. *Trogoderma granarium*. Khapra beetle. A cosmopolitan pest in warm climates. Dermestid beetles are easiest to recognize as mature larvae, when they are ~5 mm long and covered with dense tufted hairs (hastisetae). Their adults occasionally feed at flowers (Borror *et al*., 1989). Although development in this species is most rapid at high temperatures and fairly high humidities, taking 18 days at 35°C and 75% RH, it can still proceed at humidities as low as 2% RH. *Trogoderma granarium* can also carry on its life functions normally at temperatures as high as 40°C. Interestingly, there is a genetically determined polymorphism for diapause, the inception of which is brought about by adverse conditions.

6.3.1.2(h) COLEOPTERA; Dermestidae. *Dermestes maculatus*. Cosmopolitan pests of stored animal products. The species is unusual among stored product pests as its main predilection is for animal products: hides, cured meats and fish, and fish meal if it is not too salty. At 35°C and 75% RH complete development takes ~30 days. The mature larvae bore into solid media, including wood, before pupation, which can be very destructive. The related *D. frischii* can destroy salt fish in storage, and tolerate meats with more than 25% salt content! Other such pests are *D. ater*, *D. lardarius* and *D. carnivorus*. All are widely distributed. Certain dermestid beetles are associated with the final stages of degradation of human corpses (Section **8.3.1**). Scavengers such as *D. caninus* can be used to clean vertebrate skeletons for study.

6.3.1.2(i) COLEOPTERA; Anobiidae. *Lasioderma serricorne*. Tobacco beetles. Broad-spectrum pests. Apart from destroying tobacco, the larvae also attack all stored grains and seeds, flour, dried cassava, pulses, dried fruit and cocoa, dried fish, books and even pyrethrum powder! They ravage packets of cigars and cigarettes in storage. The beetles can fly, are more or less cosmopolitan but more frequent in the tropics and will not breed below 19°C. Indeed, they are susceptible to low temperatures, adults being killed in <1 week at 4°C. The life cycle takes 25–35 days under optimal conditions of about 32°C and 65% RH, but in adverse environments it can be as long as 4 months. The adults are short lived compared to many stored product beetles, do not feed and have a low AF of ~50–100. The clerid beetles *Tenebroides mauritanicus* and *Thaneroclerus buqueti* eat them. A similar anobiid pest is the drug store beetle, *Stegobium paniceum*.

6.3.1.2(j) LEPIDOPTERA; Pyralidae. *Plodia interpunctella*. Indian meal moths. Cosmopolitan in warm climates. This moth is easy to identify, having coppery brown forewings with cream coloured bases, and relatively large hindwings. The wingspan averages 16 mm. *Plodia* infests a wide variety of stored products, including grain, flour, dried fruits, nuts and even chocolate. The larvae make silken tunnels within the medium and webby silk over its surface. The adults live for ~2 weeks and do not feed. Optimum conditions are roughly 30°C and 70% RH, when females lay ~400 sticky eggs. In true lepidopteran fashion, the mature larvae wander away from the food to find pupation sites.

The life cycle takes ~27 days on adequate food under these physical conditions, rising to 52 days when the temperature is 20°C. Development ceases at 15°C. Some strains of *P. interpunctella* show larval diapause in response to decreasing photoperiod, low temperature or crowding. Several wasp parasitoids may attack these moths, including *Trichogramma evanescens* (Trichogrammatidae), *Venturia canescens* (Ichneumonidae) and *Bracon hebitor* (Braconidae). Predators include the bug *Xylocoris flavipes* (Anthocoridae) and even *Tribolium castaneum*. Granulosis virus (PiGV), *Bt* and the protist *Nosema* may infect the larvae, and cannibalism among them may augment the spread of these pathogens.

Secondary pests

6.3.1.2(k) COLEOPTERA; Silvanidae. *Oryzaephilus surinamensis*. Saw-toothed grain beetles. Another broad-spectrum pest. These are cosmopolitan, generalized feeders on stored products, following primary pests such as *Sitophilus* and *Sitotroga*. They feed only on fine granular debris formed by primary species, or enter damaged grains. Like *T. confusum*, their minute size (3 mm long) allows them to penetrate the smallest cracks, but they cannot breed below 18°C. Optima are ~32°C and ~80% RH under which conditions development takes ~35 days. The generally flightless adults, however, may live as long as 3 years. The females range widely in their AF from 50–350 eggs. Merchant grain beetles, *O. mercator,* are more widely distributed in warmer climates than their congener, and can fly. Although *O. surinamensis* can survive brief periods of subzero temperatures, *O. mercator* is soon killed at 5°C. *Ahasverus advena* is a related pest of grain.

6.3.1.2(l) COLEOPTERA; Tenebrionidae. The family is large and cosmopolitan, there being over 10,000 described species of which >100 have been associated with stored commodities. Two main pest genera are *Tribolium* and *Tenebrio*, which are found in all stages in a variety of stored products. Their larvae are easily distinguishable from others in this medium, being somewhat similar to wireworms (Elateridae, Section **3.2.1.2(a)**). The larvae of the omnivorous cleroid beetle *Tenebroides mauritanicus*, the cosmopolitan 'cadelle', which may be found with them, has the same general shape, but the advantage of being predatory. Several adult tenebrionid beetles are flightless, so that their main mode of redistribution is with the stored product.

6.3.1.2(m) COLEOPTERA; Tenebrionidae. *Tribolium castaneum*. Red flour beetles. Generally secondary, broad-spectrum pests that are cosmopolitan in warm climates. This important pest may have originated in India but is now found from South Australia to southern Europe and in the southern states of the USA. The adults are reddish-brown and often found in farm grain stores. Apart from grain, they attack a variety of other stored products. They are also cannibals, and eat other pests found therein. At 11% moisture, development takes ~35 days at 30ºC and ~25 days at 35°C, while minima and maxima for development are 22°C and 40°C. AF is 400–500 eggs/female. But there are dispersive and non-dispersive, genetically determined strains in which these characteristics vary (Ben-Shlomo *et al.*, 1991). The former does better as a colonist, but flies only under warm conditions. The latter does better as conditions deteriorate. Both larvae and adults feed on grain. Adults can live for a year at modest temperatures and their survival is increased if they are able to eat other insects. Although some populations possess an autosomal 'killer' factor that under certain circumstances results in the death of young larvae (Burt and Trivers, 2006), the demographic properties above normally give them the highest potential rate of increase of any stored product pest.

6.3.1.2(n) COLEOPTERA; Tenebrionidae. *Tribolium confusum*. The confused flour beetle. This beetle may be originally Ethiopian. It is more tolerant of cooler conditions than *T. castaneum* and has a more northern distribution. While the adults are flightless their great longevity and small size enable them to breach the defences of all but the most secure stores. AF is a little less than that of its congener but is achieved at lower temperatures. Again, cannibalism is an important source of mortality at high density. *Tribolium destructor* and *T. madens* both have a greater preference for cooler situations than the above two species.

6.3.1.2(o) COLEOPTERA; Tenebrionidae. *Tenebrio molitor, T. obscurus*. Cosmopolitan 'meal worms'. The adult beetles are blackish and the larvae waxy yellow. They are resistant to low temperatures but are of small importance as pests of stored products because their rates of population increase are so low. Both the larvae and adults of the former species can absorb water from the atmosphere, but it is probable that many beetles of stored products can do this. Several other genera of tenebrionid beetles are found in grain stores.

6.3.1.2(p) LEPIDOPTERA; Pyralidoidea, Phycitidae. *Ephestia* (= *Anagaster*) *kuehniella*. Mediterranean flour moths. Another broad-spectrum pest. This species attacks flour, stored grain, pulses and dried fruit. Unlike any of the beetle pests, these and related moths are quickly detected by the masses of silk and cocoons they produce. Their larvae also destroy any bags, a serious component of the destruction, since it entails extra material and labour costs. The ideal physical conditions for *E. kuehniella* are 28°C and 70% RH under which conditions some 200 eggs/female are laid and the generation length is ~8 weeks. But if the pupae experience temperatures >27°C an increasing proportion of the females lay no eggs, and >30°C they are almost sterile. This and the next species are attacked by the parasitoid *Venturia* (= *Nemeritis*) *canescens*, an ichneumon afflicting several pyralid moths.

Ephestia elutella, the almond moth, and *E.* (= *Cadra*) *cautella*, the fig moth, are worldwide and as well as cereal and other products, attack dried fruits and nuts in storage. They are greyish-brown with a wingspan of ~16 mm. *Ephestia elutella*, however, is better adapted to temperate conditions than *E. cautella*. It has optimum requirements of ~30°C and ~70% RH for a life cycle of ~30 days. In cool environments the last larval instar can diapause. *Ephestia cautella* has optimum requirements of ~33°C and ~70% RH, when the life cycle lasts ~22 days. A similar pest, found mainly in the humid tropics of South and South-East Asia, is *Corcyra cephalonica*.

6.3.2 Sucking pests

We have already considered a number of sucking pests of roots, stems and apical leaves. But a few species typically attack fruits and seeds although they may feed on other plant parts if their preferred food is not available seasonally. In the Heteroptera several genera in the Pyrrhocoridae, Coreidae, Lygaeidae and Pentatomidae transmit plant pathogenic trypanosomes of the genus *Phytomonas* (Camargo, 1999) and phytopathogenic bacteria and fungi (Schuh and Slater, 1995; Schaefer and Panizzi, 2000).

6.3.2.1(a) HETEROPTERA; Pentatomidae. *Nezara viridula*, *N. antennata* and *Acrosturnum hilare*. Green stink bugs. Pantropical, tropical and warm-temperate, broad-spectrum pests. Some other pentatomid bugs. These species, like many phytophagous Heteroptera, are primarily pod, seed and fruit feeders, but they also suck stems and leaves, although these are inferior foods that may not allow them to reproduce. Both *N. viridula* (Fig. 6.7) and *A. hilare* are multivoltine, the number of generations being dependent on temperature. However, in Japan *N. antennata*, which is confined to Asia, has a summer diapause and is more tolerant of cooler weather (Tougou *et al.*, 2009). *Nezara viridula* males may compete aggressively with those of *N. antennata* for *N. antennata* females, even though the latter then produce infertile eggs. The smaller *A. hilare* can be an important pest of cotton in the Carolinas, USA. *Nezara viridula* has a tropical and sub-tropical distribution, even stretching across the Pacific islands into Australia, and has up to eight annual generations.

Despite their cryptic coloration and spiny thorax, adult *Nezara* also contain a battery of foul-smelling defensive compounds including E-2-hexanal. In higher latitudes, such as in Japan and the Carolinas, the adults diapause in winter, seeking shelter in plant debris. There is a wide range of food, both in the dicots and monocots, and although there is some preference for legumes, over 150 plant species in 35 families are attacked. Seasonal changes occur in their diet. It comprises mainly young shoots early on and later in the season the fruits and seeds of important crops such as rice, cotton, soya, lima and red beans, warm-temperate top fruits and also tomatoes. Several studies (Mitchell, 2004) show

Fig. 6.7. The green stink bug *Nezara viridula* (Pentatomidae), a pantropical pest, mainly of fruits and seeds. Source: Wikimedia Commons, credit to author Quartl.

that *N. viridula* transmits phytopathogenic bacteria, including *Pseudomonas* and *Curtobacterium* of soya beans and *Xanthomonas* in cowpeas. These also cause cotton bolls to rot. In the Caribbean it may transmit the fungus *Nematospora colyli*, which affects cotton bolls similarly. But they also contain vertically transmitted endosymbionts that enhance fertility (Feldhaar, 2011).

As in *Heliothis* (Section **6.2.1.2(d)**), wild plants are critical for the maintenance of *N. viridula* populations. The berries of some privets, such as *Ligustrum lucidum,* and the pods and seeds of the extensive tropical genus *Crotalaria*, provide ideal wild food. They do not reproduce on all the species they feed on, however, castor beans and wheat being such examples. Rather unusually, females are attracted to their mates by male pheromones. Adults are also attracted to light traps. A big female has a maximum potential fertility (MPF) approaching 500, and the barrel-shaped eggs are deposited in compact, sub-triangular masses of ~12–18. They are pale yellow at first, turning pale orange (if fertile) and finally purplish before eclosion. First nymphal instars are black and yellow and remain tenacious to the remains of the eggs from which they hatched; second instars are grey/green and actively disperse many metres from their natal point. Development takes ~35 days under ideal conditions.

Egg parasitoids include *Ooencyrtus submetallicus* (Encyrtidae) and *Trissolcus* (= *Asolcus*) *basalis* (Scelionidae). The latter wasp is attracted to leaf volatiles bearing eggs, but eggs older than 4–5 days are unattractive, so that there is a rather brief window of opportunity (see references in Hilker and Meiners, 2006). This wasp is a complex and includes *T. crypticus* and perhaps other cryptic species (Section **1.3.4**) so caution is needed in interpreting data. The tachinid flies *Trichopoda* spp. attack the large nymphs and adults but are especially attracted by the pheromone emitted by adult males. This hotchpotch of parasitoids has been used with some success in South Australia and Hawaii. Despite this, *Nezara* is presently threatening the extensive macadamia nut industry in Hawaii. Mowing weeds under the trees, on which the bugs feed initially, reduces their numbers, although they feed on excised and fallen nuts too. Also, *Nezara* has become an important pest of sweet corn in Auckland, where trials with new insecticides, such as lambda-cyhalothrin and methamidophos, show that timing of the application is critical (Rea *et al*., 2003). Neem extracts (Section **13.2.3.2**) have been successful against this bug on crop legumes. *Nezara* can be captured in traps using specific pheromones. In California, the bug *Euschistus conspersus* is important on processing tomatoes. A European bug rather similar to *N. viridula* is *Palomena prasina*. It imparts a bad smell to raspberries and causes fruit distortion to apples and pears. In parts of Central and East Africa the pentatomid bug *Antestiopis orbitalis* affects coffee.

The related *Oebalus pugnax* feeds on the developing grains of rice, maize and sorghum in the southern USA (Espino *et al*., 2007) and extends into the Caribbean. Rice attacked in this way is called 'pecked or pecky rice', and naturally is an inferior product. In some rice cultivars, feeding by *O. pugnax* may make the plants more susceptible to fungi such as *Tilletia horrida* (kernel smut) and *Sclerotium oryzae* (stem rot). Other pentatomid grain bugs are included in the genera *Aelia* and are found in southern Europe. In Asia, *Eysarcornis* spp. and *Lagynotomus* attack rice, while *Halyomorpha halys* can transmit witches' broom phytoplasma between *Paulownia* trees. *Tibraca limbativentris* attacks rice in Brazil and as in *Nezara* the males produce a sex attractant. Other pentatomid genera may (*Macropygium*), or have been shown to (*Lincus* spp.), transmit *Phytomonas staheli*, which cause marchitez disease of palms (Camargo, 1999). *Lincus spathuliger* may transmit the *Phytomonas* causing phloem necrosis of coffee, while *L. croupius* and *L. styliger* are closely associated with a similar flagellate causing bronze leaf wilt of coconut (Dollet, 1984).

6.3.2.1(b) HETEROPTERA; Pentatomidae. *Biprorulus bibax*. Spiny citrus bugs of Australia. This bug is a good example of a pest that has extended its range and importance in recent years, although it is still confined to Australia. It originally fed on wild desert limes, *Eremocitrus glauca*, but with the extension of the citrus industry it has spread from Queensland to New South Wales, Victoria and South Australia. It particularly affects lemons and mandarins, but finds overwintering sites on oranges and grapefruits. Pest densities of over 10,000 adults/ha have been recorded. There may be a summer diapause during the period when the lemon trees are not in fruit. The eggs are laid in batches and the first nymphal instars have been seen feeding on sibling eggs: cannibalism within the family.

Several rather similar bugs are *Monostira unicostata* (Tingidae) and the mirid bugs *Capsodes sulcatus* on grapes; *Closterotomus fulvomaculatus* on hops and pome fruits, *Lygocoris rugicollis* on apples and *L. pabulinus* on many fruits, occur in Europe and North America (Alford, 2007). Some also feed on other insects.

6.3.2.1(c) HETEROPTERA; Pyrrhocoridae. *Dysdercus* spp. Cotton Stainers. Vectors of the staining fungus *Nematospora*. Pantropical pests of cotton bolls under humid conditions. Several species of *Dysdercus* suck cotton bolls and transmit the fungi *Nematospora gossypii* and *N. coryli* that damage the lint. They often immigrate from nearby Malvales such as *Hibiscus*, *Thespesia* and *Abutilon*, on which they survive the out-of-crop season. In West Africa the migrations of *D. voelkeri* and *D. melanoderes* have been linked to movements of the Inter-Tropical Convergence Zone (Duviard, 1977; Section **2.2.2.1**). They are effective if ungainly fliers. Marked adults are recorded moving as far as 15 km, which suggests transport on local winds. These bugs are usually some combination of red, brown and black and easily identified by their flagrant habit of remaining in copula for extended periods, another probable case of avoiding sperm competition (Section **8.2.2.3(a)**). The eggs, which are finally orange, are laid in crevices in the soil in batches of up to 100. As in *Nezara*, the nymphs remain in a cluster until they disperse in the second of the five nymphal instars (Matthews, 1989). They are particularly sensitive to the quality of their food. The tachinid genera *Bogosiella* and *Acaulona* parasitize the larger ones and the adults, but do not restrain this pest's population within a crop.

6.3.2.1(d) HETEROPTERA; Scutelleridae. *Eurygaster integriceps*. Sunn pest. An important pest of cereals in Iran, much of the Middle East and south-east Europe, attacking developing grain. This bug, which has several salient ecological features, is found on wheat and barley from Eastern Europe (Romania, Russia and former Yugoslavia) through to Pakistan (Potts, 1990), with adult densities exceeding 70/m^2, far above the economic injury level (Section **13.1.1**). New generation adults spend 9–10 months in pre-reproductive diapause when grain is unavailable (Iranipour *et al*., 2011), during which time the greater part of the generation mortality occurs, particularly to males. A special feature of its ecology is the regional variation in migration. In warmer places the adults fly up to 30 km into mountainous areas (as do some coccinellid beetles), while in cooler places they remain near the cereal fields. Successful re-migrants feed on developing grain and then lay several batches of 2–30 eggs on the plants. Laboratory estimates give a ~200 MPF. The eggs are attacked by *Ooencyrtus telenomicida* (Encyrtidae) and four species of *Trissolcus*, including *T. vassilievi, T. grandis* and *T. basalis* (Scelionidae). *Trissolcus grandis* tends to be the most numerous parasitic wasp at low pest densities.

Development through five nymphal instars takes ~6 weeks. At high density, nymphs and adults compete strongly for the quality food that grain provides, after which emigration from the crop takes place. Compromised individuals, as expected, survive winter poorly and are less fecund if they do so. Over winter, the mean weight of adults sampled in the field declines from ~140 mg to ~105 mg, but this value is partly offset by higher mortality in small bugs (Radjabi, 1995, in Iranipour *et al*., 2011). Later, parasitism by several tachinid flies, including *Ectophasia crassipennis*, *Elomyia lateralis* and *Heliozetha helluo*, reduces AF considerably, although encapsulation is frequent, particularly by young adults. Density-dependent mortality of the adult bugs occurs, with superparasitism by these flies (Section **8.2.2.5**) being general. The crop is damaged both by direct feeding but also by injection of saliva, as is common in Heteroptera. When damage affects >2% of the grain it becomes unsaleable (Radjabi 2000, in Iranipour *et al*., 2011), but presumably can be used as animal food. Crops are currently sprayed as a necessary control, but IPM (Section **13.3.2.2**) is being researched.

6.3.2.1(e) STERNORRHYNCHA; Coccoidea, Diaspididae. Armoured scales. *Aonidiella aurantii*. Red scales. Some other diaspidid scales. Cosmopolitan pests of citrus and other plants. Murdoch and his co-workers have worked hard and long on the theory and practice of biocontrol of this species (Murdoch *et al*., 1987, 1995, 1996, 1998). Such intensive studies compare with those on locusts, spruce budmoths and winter moths. Much has been learnt into the natural complex of interactions between parasitoids and their hosts. In the early years, however, time and money were wasted because of misidentifications, both of the scale and of its parasitoids (Walter, 2003). In particular, the yellow scale, *A. citrina*, was not distinguished from

A. aurantii until 1937. Good, searching taxonomy is critical for ecology.

Aonidiella aurantii is a small, reddish-brown scale, most commonly of citrus. Although it is especially important on fruits, the marketable product, it is also found on leaves and twigs. The largest mature scales occur on the fruits, intermediate ones on the leaves and smallest ones on the twigs (Luck and Podoler, 1985). Scales develop a little faster and produce larger adult females on lemons than on other citrus, but they infest a wide variety of other plants including yucca, *Yucca filipendula*, castor beans, *Ricinus communis*, and even sago palms, *Cycas revoluta* (Smith, 1957). On citrus, severe attacks cause die-back of branches and destruction of the fruit. Diazinon and malathion were traditional sprays, but chlorpyrifos, methidathion and carbaryl are used now, while mating disruption techniques have been researched recently. But biocontrol using the aphelinine wasp *Aphytis melinus*, which is indigenous to the Indian sub-continent, is now the preferred method, although *A. chrysomphali* and *A. lingnanensis* had been tried earlier. Insect growth regulators (Section **13.2.3.2**) may supplement *A. melinus*. These parasitoids oviposit under the protective scale and, having a shorter generation time than their host, have been effective in suppressing its numbers. They oviposit mainly on peripheral scales (Walde *et al*., 1989; Murdoch *et al*., 1995), leaving those attacking structural branches relatively untroubled. This choice may result from differences in illumination, but scales are on average smaller centrally and *A. melinus* prefers larger ones. Hence, central scales are in a partial refuge (Section **9.9**). This should add stability to the interaction, but evolutionary forces will also be at work.

Red scales are host to several other Parasitica, including *A. lingnanensis* (above), which may be driven to extinction by *A. melinus*. Others include *Encarsia perniciosi* (Aphelininae) and *Comperiella bifasciata* and *Habrolepis rouxi* (Encyrtidae). Some of these are adversely affected by the type of food scales consume (Smith, 1957). *Encarsia perniciosi* has three forms: a thelytokous form afflicting *A. aurantii*, and thelytokous and arrhenotokous forms parasitizing *Quadraspidiotus perniciosus* (Stouthamer and Luck, 1991, in Sullivan and Völkl, 1999). *Chilocorus* spp. (Coccinellidae) eat these scales, so destroying their endoparasitoids. *Aspidiotus destructor* is the pantropical coconut scale, also found on mangoes and bananas, *Fiorinia theae* attacks tea, and *Unaspis citri*, the snow scale, is a widely distributed pest of citrus.

6.3.2.1(f) STERNORRHYNCHA; Coccoidea, Coccidae.

Soft scales. *Lepidosaphes beckii*. Mussel scales. So named because of their shape, these are also citrus scales but attack croton bushes as well, to which citrus is unrelated. After the first instar crawler stage, a scale develops in both sexes. Fragile, winged males may emerge from under the scale. As in red scales, branches and leaves as well as fruits are attacked, and control is similar to that for that species. In the Mediterranean Basin the soft brown scale, *Coccus hesperidum*, attacks a variety of fruits. *Coccus viridis* and *Ceroplastes destructor* and *Ce. floridensis* are other citrus pests. In the latter genus males are unknown.

7 Medical and Veterinary Pests

7.1 General Introduction

Just as our main crops are derived from a relatively few families of flowering plants (Section **2.1**), so domesticated animals belong to only a few avian and mammalian groups. While to the general public the word 'animal' often means 'mammal', as scientists such ambiguities are disallowed, so when talking about 'animals' we mean any animal be it *Drosophila melanogaster* or *Homo sapiens*. For terrestrial vertebrates we use the proper term: '*tetrapods*' (the four-footed ones). Most domesticated mammals are in the order Artiodactyla, which have cloven hooves. With their years of domestication they include sheep and goats (Caprini, >10,000 years), pigs (Suidae, 9500 years), cattle (Bovinae, 8000 years), and camels and llamas (Camelidae, 5500 years) (Diamond, 1999). Horses and donkeys are Perissodactyla, rabbits are Lagomorpha and cavies (guinea pigs) are caviomorph rodents. Other such vertebrates comprise several families of birds and fishes, while a few invertebrates such as molluscs (oysters), crustaceans (lobsters) and insects (bees and silk moths) have been cultured from ancient times (Section **8.3.3**). Insects attack all terrestrial domesticated animals, of which mammals are clearly the most important economically. All these animals, like plant cultivars, are products of selective breeding, and hence differ materially from their wild relatives in appearance, physiology and behaviour. Their human domesticators, being mammals, are naturally vulnerable to many of the pests, or their close relatives, that attack livestock, a fact linking veterinary and medical entomology.

While there are several parallels between the ecology of insects attacking plants and those attacking domesticated animals and ourselves (Price, P.W., 1997; van Emden and Service, 2004), we treat them separately. A commonality is that insects transmit pathogenic organisms: nematodes, fungi, bacteria, viruses, phytoplasmas and occasionally protists between plants; nematodes, protists, bacteria and viruses between animals (Section **1.6**). We are concerned mainly with the Diptera here, plus a few small orders such as lice and fleas. The diseases insects transmit are often more virulent than those caught by other means (McNeill, 1976), who suggests that the pathogen evolves to be tolerated better by the vector than by the vertebrate host, since a healthy vector is necessary for effective transmission. A further hypothesis is that the parasite evolves increased severity in its vertebrate host (Ewald, 1983). In all, *parasites evolve to manipulate vectors*, especially their host-seeking abilities, for their own ends (Hurd, 2003). But in this the vector's fecundity may be reduced (Section **7.3.2.4 (d)**), and the victim, whether plant or animal, may then be predisposed to infections not carried by the vector itself.

The broad term disease (meaning 'dis-ease') refers to loss of condition of an organism whether caused innately, such as the outcome of genetic defects, or extrinsically by a pathogen. For plants, disease has been defined as '… responses of plant cells to a pathogenic organism …' (Agrios, 2005). So a pathogen is a foreign organism causing disease. But the definitions are not entirely clear as the results of herbivory would not be regarded as a disease, nor would a herbivorous mammal be viewed as a pathogen! Pathogens are tacitly micro-organisms that multiply rapidly in their victims, as in the term *pathogenic micro-organisms*. Tetrapods have low reproductive rates relative to the insects that attack them, whose numbers may vary rapidly and widely in size. This means that a victim species may be attacked by numerous noxious insects at one time and hardly by any at all at another; but there are other consequences (Hamilton, 1980; Section **11.2.3.1**). Similarly, some plant pests are typically sporadic, which makes it difficult to predict their attack.

Animal food is nutritious while plant food, apart from nuts and seeds, is of poor quality (Section **9.8**). Although low quality can be regarded as a

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general component of a plant's defences, these normally involve special physical or biochemical mechanisms (Section **2.4.2**). As we have seen, plants possess no true immune system, namely one that can recognize foreign proteins. Tetrapods do possess such mechanisms and this, with the added feature of movement, makes them more demanding on potential enemies. These are key points in appreciating the considerable differences that exist between the taxonomy, ecology and behaviour of insectan pests of plants and those of animals. Tetrapod movement has two aspects: (i) locomotion, which the potential insect pest has to match in terms of searching and finding, or in default of this by having, like cestodes, huge numbers of progeny (Section **10.2.4.1**); and (ii) grooming, by which the bird or mammal can rid itself of resident vermin. These are capabilities hardly possessed by plants and as a probable result, medical and veterinary pests *are found in far fewer insect orders* than are those attacking plants. In fact, the Diptera contains their large majority. The message for potential medical or veterinary entomologists is that they should understand the biology of this order pretty well. Additionally, hosts can be regarded as resource 'islands' for pathogenic micro-organisms, a similar concept to that of patches or habitats for insect pests of plants (Anderson and May, 1992; Section **12.2**) and comes under the umbrella of the *metapopulation* concept (Sections **9.5** and **12.3**).

Pests may gain access to mammals and birds either when they are at rest (especially in nests and lairs) or in mutual contact, as bugs, lice or fleas do, or by pursuing them as do most Diptera. It is no coincidence that this order includes so many mammalian pests because, typically, they have adequate sensory and flight capability to track and pursue victims. If you go into a damp woodland on a summer's day most of the flying insects are Diptera. The unique flight control systems of flies 'enable them to detect and respond to moving targets with rapidity' (Chan *et al.*, 1998). The piercing and sucking mouthparts present in many adult flies are a subtle means of attacking a much larger animal, organ systems they have in common with bugs, most lice and fleas (Section **1.4.1**). Other insect orders contain virtually no mammalian or avian pests, and it is odd that although numerous Hymenoptera attack other insects (Gauld and Bolton, 1991), they have not evolved to affect any living tetrapod, except, of course, by stinging them if threatened. Also, while both the Diptera and Hemiptera are large and diverse orders containing numerous genera with piercing mouthparts, adult Diptera, unlike most bugs, never use these organs to suck plant sap, although they often imbibe nectar. Again, taxonomy has links with ecology. Then, very few insect families contain species specialized to attack plants on the one hand, and tetrapods on the other, suggesting long evolutionary specializations. An exception, however, is the diverse family Muscidae in which, for example, the beet leaf miner and the cabbage root fly attack plants, tsetse and biting stable flies attack mammals, and *Acridomyia* is a parasitoid of grasshoppers.

Most dipteran vectors are tropical, largely because the order is more diverse in the tropics and that pest eradication and the modification of the environment for agricultural purposes generally have been less radical there than in temperate regions. But the fact that active adult dipteran vectors are present throughout the year in the tropics, but not in cool temperate regions, is significant. Potential vectors do fly in cold weather.

There is no sound ecological reason for separating these pests into human and non-human types. Indeed, several groups and even species transmitting diseases attack both ourselves and our livestock, as in mosquitoes and tsetse. Human societies beginning to domesticate mammals were afflicted by mutant strains of diseases of these beasts (Diamond, 1999). While medical doctors treat us and veterinarians treat our animals, economic entomologists link these two areas of human endeavour. So we will consider insects of medical and veterinary importance together. Nor is there a sound case for dividing these pests into vectors and non-vectors. At the beginning of the twentieth century few insects were known to transmit diseases, but since then more and more, including some quite recently, have been found to have this capability: there is still a chance that a supposed non-vector will turn out to transmit a pathogenic micro-organism. A better scheme is to classify the pests by their mode of attack and then by their taxonomic position, one revealing some useful generalities. Classification is a useful steppingstone in the structure of science (Section **2.1**). Erasmus Darwin (1794/1796) introducing *Zoonomia* (Vol. 1) defines one of his aims as 'to reduce the facts belonging to animal life to classes, orders, genera and species; and, by comparing them with each other, to unravel the theory of diseases' (King-Hele, 1999).

7.1.1 A classification of insect pests of people and domesticated animals

Many of these beasts suck blood and are often broadly termed 'haematophagous insects'. In those that take large meals, there are periodic physiological episodes of ridding the body of excess water and nitrogen (Willmer, 1982). Despite earlier classifications in which free-living forms such as mosquitoes and tsetse are called parasites (Waage, 1979), here we separate these *micropredators* from true *ectoparasites* because of the clear distinctions in their taxonomy, structure, biology and ecology, as follows.

7.1.1.1 Ectoparasites

Such insects form a long-term association with an *individual* host, living on it, being modified for so doing, having strong legs and stout claws for clinging. They feed insistently on their host and usually cannot survive away from it. They are small or rarely of medium size. Small size (Section **1.2**) means they can be numerous and hard to detect. Their bodies are tough and flattened, laterally in fleas and dorsoventrally in lice and keds. These features are defences against grooming. *Both sexes bite* and, apart from most bird lice, have piercing and sucking mouthparts. As adults they have lost or lose the ability to fly. Their juveniles are either also present on the host, and have a similar lifestyle to the adults (lice), or develop in close association with it (most fleas). They cause loss of the host's condition and may transmit bacterial and occasionally viral diseases in infective faeces, or by biting a new host. The human diseases they transmit (typhus and plague) have been severe and episodic, and while not confined to temperate regions seem to have been more significant there. Unlike temperate micropredators, ectoparasites bite all year long and are generally *multiplicative vectors* (Section **7.1.1.4**). The continuing and intimate association between ectoparasites and their hosts entirely alters the spatial dynamics and hence genetics of their populations relative to micropredators and flies causing myiasis.

7.1.1.2 Micropredators

While a true predator potentially kills its prey a micropredator does not, devouring only a small fraction of its blood. Excepting a few exopterygote examples in the triatomine and cimicid bugs, which are to an extent transitional to ectoparasites, micropredators comprise endopterygote, biting flies. They attack only as adults, flying to seek prey and to escape, and always retaining effective flight. The adults and juveniles have *very different lifestyles* and population ecologies from those of ectoparasites and show little intimacy with their prey. Indeed, they have *individually* far greater powers of searching and finding (Section **10.2.4.1**) than ectoparasites. But they require mild or warm weather to do this and although there are several exceptions they are more common in the tropics than at higher latitudes. There is a brief and sneaky attack episode by the small assailant who lives elsewhere. Except in the Cyclorrhapha, only *the females bite*, this sex alone having piercing mouthparts. Micropredators often feed sequentially on the blood of *several prey* individuals, and have elaborate sensory–motor systems to locate them. So they are *predisposed* to be vectors and indeed transmit a wide range of protistan, filarial, bacterial and viral organisms, often paying a cost in that these pathogens may cause their decline or premature death. They tend to be specific, thus only *Anopheles* mosquitoes transmit malaria and only tsetse spread sleeping sickness. These biting flies belong to the Nematocera in particular, but also to the Brachycera and Cyclorrhapha. They are of all sizes, from *Culicoides* midges of <1 mg to tabanid flies of >200 mg body mass. They often cause stress to their prey and may be either mechanical or multiplicative vectors. Indeed, the only similarity between ectoparasites and micropredators for us is that they have piercing and sucking mouthparts and transmit pathogenic micro-organisms. The term 'haematophagous' fails to distinguish the many and significant ecological differences given here, and that micropredators are a more frequent cause of disease transmission in the tropics. Ectoparasites are not a phase in the evolution of micropredators, but represent separate evolutionary lines.

7.1.1.3 Flies causing myiasis

Myiasis is the infestation of a living vertebrate, usually a warm-blooded tetrapod, by *dipteran larvae*, these being the maggots of the Cyclorrhapha. Unlike ectoparasites and micropredators they frequently kill their victims directly. Myiasis differs from other forms of parasitism since a free-living, adult female distributes her progeny to several vertebrate hosts, where they feed within living tissue. The tissue affected may be dermal, as with the strike flies *Lucilia*, or internal as with horse bots *Gasterophilus*. This is more like the lifestyle of some insectan parasitoids. The larva of the calliphorid fly *Auchmeromyia*, the Congo floor maggot, provides an interesting exception. It is a leach-like external blood sucker, visiting its victim only for meals (Section **7.4.1.2(a)**).

Cyclorrhaphan flies causing myiasis are in the highly evolved families Calliphoridae, Muscidae and Oestridae. They are all excellent fliers, usually of medium size (~40–80 mg) and often stress potential hosts by chasing them. Their mouthparts are not piercing and hence the adults are never micropredators and never transmit microbial diseases, except sometimes by contamination. They deposit either eggs or young larvae. The developing larvae consume either the host's tissue fluids (warble flies) and give rise to further stress, or its living tissues (sheep strike flies) in which case they normally cause its rapid death unless treated. Species feeding only on living tissue exhibit *obligate myiasis*; those that also breed on carcasses exhibit *facultative myiasis*. The distinction is important ecologically as the latter group can maintain or increase population size by consuming dead animals. The sheep strike flies *Lucilia* may build up their numbers on discarded still-born lambs.

The consumers of living trophic resources, like those above, may be classified on two independent scales: *lethality* and *intimacy* (Stiling, 1999). In the present case, ectoparasites are low on lethality but high on intimacy, while micropredators are low on both scales. In contrast, maggots causing myiasis are usually high on both scales. Both the above classification of vertebrate pests and those of Marshall and Stiling, which were made independently, show mutual support. Note, of course, that the pathogenic micro-organisms that may be transmitted, certainly the ones that infest people, are typically high on both scales.

7.1.1.4 Some additional points

To recap, both ectoparasites and micropredators may transmit pathogenic micro-organisms. The former insects may do so in their infective faeces (lice and fleas), or when they leave their original, infected host and bite a new one (mainly fleas). Micropredators tend to be more efficient vectors as they frequently bite several host individuals. Excepting reduviid bugs, their faeces are not infective. Pathogenic transmission is essentially of two types. First, purely mechanical transfer, when the pathogen does not multiply in the vector. This transference requires meals to be taken on more than one victim in a short space of time. Second, that which is also primarily mechanical but is followed by the pathogen multiplying in the vector. Tabanid flies are mechanical vectors, but plague fleas and malarial mosquitoes are multiplicative vectors. In the latter case there is a *latent period* in which the pathogen is multiplying in the vector. During this time some mortality of the vector and hence of the micro-organisms occurs. For *Plasmodium* 8–13 days, but in Yellow Fever Virus only 4–5 days, are required before the mosquito becomes re-infective (Service, 2000). This is significant in the epidemiology of such diseases (Anderson and May, 1992; Fialho and Schall, 1995), because the vectorial capacity is increased by the shortness of the latent period. A similar distinction applies to the transmission of plant viruses, with non-persistent types that exist briefly on the vector's mouthparts and persistent types that multiply within them (Ossiannilsson, 1966; Section **5.3**). Although a large number of Diptera bite tetrapods, and another group causes myiasis, there is none that bites (and may be vectors) *and* causes myiasis (but see *Dermatobia,* Section **7.4.1.1(d)**).

For greater information on medical entomology, one should consult the handy book by Service (2000). Cox (2002) gives a concise and readable account of human parasites. Medical and veterinary entomology are covered in Lehane (1991), Kettle (1995) and Mullen and Durden (2002), while Garrett (1994) considers our fate in *The Coming Plague*. Eldridge and Edman (2003) deal with epidemiology and economic control.

7.2 Ectoparasites

7.2.1 Exopterygota

In ectoparasitic exopterygotes all instars are present on the host, so forming a sub-population or better a tribe, in which the individuals show greater mutual relatedness than a random collection from the population. Related individuals are likely to show different behaviours, particularly co-operation, towards each other than are unrelated ones (Hamilton, 1964; Trivers, 1985). One should bear this in mind when investigating such insects.

Firstly, we consider lice, which may have had free-living ancestors resembling Psocoptera (Waage, 1979).

7.2.1.1(a) MALLOPHAGA. Biting lice. Cosmopolitan pests, usually of birds, occasionally of mammals. Most of the 3000 known species attack birds and are usually highly host specific. Those on birds normally have two tarsal claws, those on mammals only one. There are several genera found on poultry, including *Menopon*, *Menacanthus*, *Goniocotes* and *Goniodes* on chickens, *Chelopistes* and *Oxylipeurus* on turkeys and *Columbicola* on pigeons. But *Haematomyzus elephantis* is found on elephants and *Bovicola* (= *Damalinia*) infests cattle (*B. bovis*), sheep (*B. ovis*), goats (*B. caprae*) and horses (*B. pilosa*). *Trichodectes canis* bites dogs and can transmit the tapeworm *Dipylidium caninum* (Section **7.2.2.2(c)**). None lives on people. One study on *B. bovis* shows that the sex ratio is *spanandrous*, with males being in a minority. Such a ratio is expected from Hamilton's work (1967) on inbreeding. Indeed, lice survive poorly away from their host. Hence, it is probable that those on a given host are to an extent inbred relatives. A similar situation is expected in sucking lice.

7.2.1.2(A) SIPHUNCULATA (= ANOPLEURA). Sucking lice. cosmopolitan pests and disease vectors of mammals. These lice affect mammals. *Pediculus* and *Pthirus* (Pediculidae) feed as ectoparasites on people. Unlike their biting relatives, Siphunculata may be vectors of disease organisms to human beings, but not, apparently, to domesticated mammals, although several species are found on pigs and cattle. This is rather surprising.

7.2.1.2(b) SIPHUNCULATA; Pediculidae. *Pediculus humanus*. Human louse. An important pest and multiplicative disease vector affecting people and thriving in unhygienic conditions. Two sub-species exist: *P. humanus corporis* on the body and clothing, while the smaller *P. humanus capitus* is found in the hair of the head, with personal infestations not being co-extensive. Some workers consider these to be separate species, as they rarely interbreed, and when they do, produce various sexually intermediate forms. But head lice are sometimes found in clothing (Burgess, 2004). *Pediculus h. corporis* probably evolved recently as a result of our starting to wear clothes. The related *P. schaeffi* occurs on chimpanzees. All juvenile stages and adults are found in an infestation. Lice rapidly increase their numbers on people after an initial infection when normal personal hygiene, that is to say regular bathing and changing of clothes, lapses. Person-to-person contact normally transfers the lice and they generally desiccate within 24 hours off the host. Build-up is facilitated by a short life cycle (20–30 days), although fecundity is only 50–60. Eggs are attached to hair or clothing. Massive populations of lice typically exist on soldiers engaged in sieges and in trench warfare, as during World War One (WWI, 1914–1918). Graphic descriptions of living with lice in the Spanish Civil War (1936–1939) are given in George Orwell's (1938) *Homage to Catalonia*, a fragment of which I quote: 'Other insects, mosquitoes for instance, make you suffer more, but at least they aren't *resident* vermin. The human louse … lives chiefly in your trousers. Short of burning all your clothes there is no known way of getting rid of him'. Orwell, although correct in separating ectoparasites from micropredators, was wrong about riddance, as Russian troops had earlier deloused themselves by placing their uniforms on ant's nests! A scene to be fondly imagined. Ironing quickly kills lice, as does hot water. Medieval monks, who regarded washing with abhorrence, referred to their lice as 'Pearls of God', a euphemism if ever one existed, dangerously close to blasphemy. Lice were seen leaving the cooling corpse of Thomas Becket (1118–1170), as the holy man lay slain on the stone floor of Canterbury Cathedral. Onlookers were amazed at the extent of his piety.

Direct personal discomfort arises from heavy infestations because lice feed insistently, and the saliva they inject causes irritability and depression. One feels 'lousy'. Persistent biting also causes hardened, deeply pigmented skin, a condition aptly called 'vagabond's disease', and more elegantly 'parasitic melanoderma'.

More importantly, they transmit human diseases, of which epidemic typhus caused by the bacterium *Rickettsia prowazeki* is by far the most serious. This mechanism was suspected by Erasmus Darwin (Section **11.1.2**) in the eighteenth century and proven when in 1909, Charles Nicolle experimentally infected chimpanzees from people, and then showed louse-borne transmission between these apes (Nicholle *et al.*, 1909; Schultz and Morens, 2009). *Rickettsia prowazeki* also infects squirrels (Ewald, 1983) and the vector itself. Transmission is simple. A louse feeds on an infected person and sucks the micro-organism into its gut where it multiplies, passing out with the faeces. The louse turns red and dies prematurely (8–12 days). These faecal deposits then get into the body of another human victim, either by being scratched into the eye, a bite or abrasion, or by being ingested as contaminated food or inhaled as a dry powder. Louse faeces can remain infective for about 2 months. *Rickettsia* do not enter the human body via the louse's mouthparts while it is feeding. In the first instance, the infection route is thus similar to that in Chagas' disease by triatomine bugs (Section **7.3.1.1**), but dissimilar to that of malarial infection by anopheline mosquitoes (Section **7.3.2.4**(**d**)). The spread of typhus is also facilitated by the fact that lice leave a victim who is in a high fever, which is comparable to fleas leaving their hosts dying from plague (Section **7.2.2.2**(**b**)).

Typhus epidemics were also associated with the 1845 potato famine in Ireland and with the 'Highland Clearances' in Scotland (Prebble, 1990). In WWI, there were millions of deaths from the disease, many of them occurring on the eastern fronts and continuing during the Russian revolution. Some estimates are >20 million (Gross, 1996). In World War Two (WWII, 1939–1945) a further epidemic in Naples was averted by treating everyone's clothing with DDT dust, one of its first applications. Even so, the death toll was about 2000. Louse infestations typically built up on sailing ships where typhus episodes were referred to as 'ship fever', and may still do so in prisons and refugee camps in diverse places.

Pediculus humanus also transmits the bacterium *Bartonella quintana* (Section **7.3.2.4**(**a**)), which caused the well-named trench fever, as it occurred during WWI and during WWII on the Eastern Front. As with typhus, the faeces become infective. Few outbreaks of this disease, which is acute but rarely fatal, have occurred since then. Lice also harbour the causal organism of relapsing fever, the spirochaete *Borrelia recurrentis*, which they suck up from an infected person. This bacterium multiplies in the insect's haemocoel, but the only way to become infected is to crush lice between ones teeth! While this disease may result in as much as 50% mortality in undernourished people, typically it causes much less. While body lice are now rare in developed countries, head lice are common on school children and on some undergraduates who have moved out from the watchful eyes of their parents, like monks shunning showering and combing. Treatment is to apply synergized pyrethrum shampoo. This also rids you of the *beast below*, hopefully before your spouse, should you have one, finds out.

7.2.1.2(c) SIPHUNCULATA; **Pediculidae.** *Pthirus pubis*. Crab louse. Potentially embarrassing when found, but not serious. This louse, although having the distinction of being described by Linnaeus in 1758, derives its greater fame from its usual confinement to the human pubic area, although there is apparently a single record of it on the gorilla, which was probably *P. gorillae*. Indeed, our ancestors may have acquired it from ancestral gorillas 3–4 million years ago (Reed *et al*., 2007). It also occasionally turns up in gentlemen's beards. Apart from being a major or minor embarrassment when discovered, according to the circumstances, it does little of importance. The lice sneakily transfer themselves during human copulation, a process unlikely to be noticed at the time. This lack of disease transmission is odd when one compares it with *Pediculus*, and is certainly surprising in view of what can be transmitted by copulation itself, although there has been a speculative suggestion that it might transmit *Treponema pallidum*, the spirochaete causing syphilis. This seems unlikely since their distribution in the pubic area places them outside the mucosal regions where the primary chancre of syphilis invariably occurs. Under normal circumstances fecundity is 150–200 and the life cycle completed in ~3 weeks (Service, 2000).

Other sucking lice afflicting livestock include *Solenoptes capillatus* and *Haematopinus eurysternus* on cattle, *H. suis* on pigs and *Linognathus* spp. on sheep. Heavy infestations cause anaemia, loss of condition, lower weight gain and increased susceptibility to other diseases. These lice can be controlled by feeding a slow-release bolus of ivermectin or moxidectin, treatments also suppressing fly larvae in cattle faeces (Section **7.3.2.4**(**o**)), but it is ineffective against biting lice, such as *Bovicola bovis*, since they feed superficially on dermal products.

7.2.2 Endopterygota

These ectoparasites are present on their host only as adults, the developmental stages usually living elsewhere, as is normal in endopterygotes. Unlike micropredators most individuals spend their entire adult lives on a single host and usually lack the power of flight. It is the few that *do* change their host that can transmit disease.

7.2.2.1(a) DIPTERA; Hippoboscidae. *Hippobosca, Melophagus*. Keds. Occasional pests of horses, sheep, cattle and deer. This small family of aberrant cyclorrhaphan flies are highly modified for ectoparasitic life on mammals and birds. They are tough, flattened and have strong, clawed legs. A few, such as the sheep ked, are permanently wingless. Both sexes suck blood. Their scientific name, although a marginal misnomer, refers to their habit of nurturing single larvae, in a specially developed uterus modified from the common oviduct, and giving birth to each mature grub in a Kafkaesque fashion. Usually, the larva drops to the ground and pupates immediately.

In agriculture, the only important species is the sheep ked, *Melophagus ovinus* (Fig. 7.1). Ked bites assist sheep strike fly maggots (Section **7.4.2.1**) to penetrate their hosts more easily, leading to wound myiasis. In this species the puparia are attached to the sheep's wool (Waage, 1979). *Hippobosca equina* bites horses and cattle and may be seen in clusters between their hind legs. *Lipoptena cervi* bites deer, while *H. camelina* bites camels and sometimes their riders. In North America the pigeon fly, *Pseudolynchia canariensis*, bites fanciers and in the Orient often infests pigeons bred for food. In all, however, hippoboscid flies are not very host specific.

7.2.2.2(a) SIPHONAPTERA; Pulicidae, Lycopsyllidae, Leptopsyllidae, Ceratophyllidae, Hectopsyllidae. *Pulex, Xenopsylla, Uropsylla, Nosopsyllus, Leptopsylla, Ctenocephalides, Tunga*. Fleas. Cosmopolitan pests and multiplicative disease vectors mainly affecting mammals. These are ectoparasites of mammals or occasionally of birds, particularly of those having nests, lairs or home bases. Our relatives, the arboreal apes, and also monkeys, are naturally without these ectoparasites. They are an ancient group, being known from Cretaceous fossils and probably having origin in the Mecoptera. Fleas can be distinguished from other ectoparasites because their bodies are laterally compressed instead of being dorsoventrally flattened like the rest. They are streamlined with stout bristles projecting backwards and move with dispatch through the hair or plumage of their host, their helmet-shaped head serving to part obstructions. The prothoracic and mesothoracic segments are extremely reduced, while the metathorax, carrying the jumping legs, is relatively large. The 3000 world species vary in colour from sandy yellow to almost black. They are often specific to one or a few related hosts, but if they leave their host individual, as in the case of its demise, they will feed on other mammals they encounter. Away from a host they move by jumping.

Fig. 7.1. The flightless, ectoparasitic sheep ked *Melophagus ovinus* (Pupipara). Source: Wikimedia Commons, author Alan R. Walker.

Fecundity may be several hundred eggs per female, greater in the jigger flea. The larvae resemble those of the Diptera Nematocera in that they are legless but possess a complete head capsule. Otherwise, they are sparsely hairy, active and resist desiccation. They feed upon the fallen hair and other debris like household dust, which contains a high proportion of sloughed human skin, and also on faeces of the adults: a rather odd case of parental investment! But adults imbibe more blood than they can digest (Moser *et al*., 1991), so this behaviour is adaptive. *Ctenocephalides felis* larvae also eat flea eggs and injured larvae. This stage takes only a few weeks to develop. Peculiarly, in *Uropsylla tasmanica* in Australia, larvae live in the skin of their mammalian hosts (Waage, 1979, see *Tunga*, Section **7.2.2.2(c)**). Pupation is within a cocoon, which makes for resistance to insecticides. Adult fleas emerge within this cocoon, but usually remain there until a potential host comes along, an event that they detect by vibration (Smit, 1973) and/or by enhanced CO_2 levels. Their relatively spectacular jump, absent in lice, presumably allows their transfer from separate larval to adult micro-environments. But this is plausible conjecture (Section **11.5.1**). Some adult fleas are long lived: human fleas, *Pulex irritans*, may live >500 days (Rothschild and Clay, 1952).

The human flea, due maybe to the selective pressure exerted by our recent predilection for hygiene, is now more usually found infesting pigs, another sparsely hairy omnivore. Its original host is probably the badger, *Meles meles*. While it can transmit the plague bacillus (Section **7.2.2.2(b)**) it is not important in this connection. It does, however, transmit murine typhus caused by *Rickettsia typhi*, either from rat to rat or from rats to people (Azad, 1990). In the latter case, infected flea faeces contact an abrasion or mucous membrane. It is essentially a rat's disease spread by several of the fleas involved in plague, but also by *Ctenocephalides* and by the rat louse *Polyplax spinulosa*. Other diseases that fleas may spread include tularaemia (Section **7.3.2.4(l)**), listeriosis, glanders, melioidosis, brucellosis, which are bacterial, and viruses causing lymphocytic choriomeningitis and encephalitis.

7.2.2.2(b) FLEAS AND PLAGUE. Plague is caused by the Gram-negative coccobacillus *Yersinia* (formerly *Pasteurella*) *pestis* and is spread largely from rats and other rodents to people by several species of fleas. It was identified in 1894 by Yersin and probably evolved from the related *Yersinia pseudotuberculosis* within the last few thousand years (Hinnebusch *et al*., 2002), by developing a biochemical agent, *Ymt*, that allows it to persist, multiply in and block the flea's gut. *Yersinia* has three varieties: (i) *Y. pestis antiqua*, the original strain, found from Central Africa to Asia; (ii) *Y. pestis mediaevalis*, responsible for the Black Death and found from Central Asia to Europe; and (iii) *Y. pestis orientalis*, which is worldwide (Devignat, 1951). Gage and Kosoy (2005) using DNA studies, have separated seven strains of *Yersinia* from different rodents in different regions.

Of all insect-borne diseases, plague, together with malaria, has had the greatest impact on recorded human history. It is reported in the Bible (1 Samuel: 5–6) as smiting the Philistines. In 430 BC, it struck Athens during a siege by Sparta, reducing the population of some 230,000 considerably, the ruler Pericles losing both his sons, and finally succumbing to it himself. The Athenian scholar and general Thucydides, himself a survivor of plague, had the rare distinction of describing its course for posterity. The Antonine Plague occurred in the reign of Marcus Aurelius (161–180 AD), further decimating the Roman army. The period 249–270 AD saw another outbreak in the Roman Empire. In 542 AD plague re-emerged in Egypt, spread to Byzantium on ships carrying grain and rats, and subsequently cut a swathe through the Empire of Justinian. It persisted until the eighth century reaching as far as Denmark and Ireland, killing untold numbers of people – the figure could be as high as 100 million deaths. Its resurgence as the Black Death in fourteenth century Europe was responsible initially for the demise of >25 million people and some authorities put this figure as high as 50 million deaths. As far as Europe was concerned, this episode started in Kaffa, the port of Feodosiya on the Black Sea. It may have originated in eastern Asia and been brought west with the flea-ridden 'Golden Hordes' of Chingiz Khan and later of Batu, arriving about 1240. More likely it came along the Silk Road rather later (Ascherson, 1995). Initially, Christian Europeans thought it was a scourge on ungodly Asians. But no! Sailors and slaves brought it to Genoa in 1347. Other ports such as Marseilles, Montpelier, Barcelona and the Mediterranean islands were quickly affected. Plague-stricken ships floundered and were washed up, again spreading the disease. Immediately, the farsighted administration of Venice instituted 'quarantine' lasting 40 days (quaranta = 40) for sailors disembarking there. Even so, there, in Paris and in Florence plague killed over half the population. At the holy city of Avignon, Pope Clement VI, surrounded by fires to thwart the miasmas (below), consecrated the Rhone so that bodies could be consumed rapidly by its waters. Others, whether dead *or dying*, were committed to mass graves. It reached Weymouth in southern England in the summer of 1348, was soon in Bristol and later spread uncontrollably, reducing the population from 3.7 to 2.1 million within a few years (Hatcher, 2008).

All over England some of the place names containing the word 'bury', such as Hertingfordbury, were the sites of the mass graves of its victims. In the village of Tewin nearby, victims were buried in a pit at the end of 'Bury Lane'. But other such places are derived from the Saxon word 'burh', a fort. Plague was a contributory cause of the demise of many English villages during this period. Over 250 villages were abandoned in Warwickshire, Leicestershire and Northamptonshire where human population density was high, and trade skills were often lost. Further localized epidemics occurred until the seventeenth century, with, for example, outbreaks in Devon (1546–1547) and Staffordshire (1593). London had outbreaks in the 1520s and 1590s, but influenza (1555–1559) and famine (1596–1597) were also serious causes of human death (Guy, 1988). Plague culminated in London (1664–1665) when an estimated 98,000 people died, a fifth of the city's population. Rather worse odds than Russian roulette. Sir Isaac Newton retired to the country to avoid it. The impact on a person in the death throes of plague are captured by these lines from Günter Grass's (1978) novel *The Flounder*:

> Sick with the awful plague, ere he could pass away
> And cast his body off! For his infected blood
> Like burning fire rose upward in his head
> And seized upon his eyes, with raging fever bright.
> Speech had forsaken him, his throat was bounden tight,
> His lungs did heave and pant, th' entire frame was sick
> And losing its strength. A nauseating reek
> As of a long dead beast from out his gullet flowed.
> His poor defenceless life upon the threshold stood.

In the late fifteenth century plague struck down Giangaleazzo Visconti, Duke of Milan, as his army prepared to annex Florence, changing the course of the Renaissance. In Perugia between 1424 and 1486, eight epidemics of plague occurred. Over the four centuries at least 125 million Europeans died of plague. Episodes were so severe in England that by 1525 the population was only 2.26 million. Even by the 1690s the population was only ~5 million (Wrigley and Schofield, 1981, in Guy, 1988), a quarter that of France. The deficit of population naturally had a major influence on British foreign policy and led to a further strengthening of the navy. Ireland became denuded of oaks, with which to build ships, and has few of them today. Such were the socio-political and ecological ramifications of disease borne by a mere insect.

The last major episode in Western Europe occurred in 1720–1721 in Marseilles, killing half the population of 100,000. French workers have extracted *Y. pestis* DNA from the tooth pulp of buried victims, thereby confirming the nature of the outbreak, as some workers have proposed other micro-organisms caused this and other episodes of plague. Recent re-occurrences of plague have been in India, where the last epidemic from 1898–1918 was responsible for several million deaths. The benign Hindu attitude towards rats: Lord Ganesh, son of Shiva is pictured with rats scampering playfully at his feet, does not help in the matter. In 1942 the Japanese, fighting the Chinese in Manchuria, released *Yersinia*-infected fleas on their opponents: both armies caught plague. China, Botswana, Madagascar, some parts of South America and even the western half of North America have also had outbreaks. In the latter region, the main vector is *Oropsylla montana*, a flea found on wild rodents and, hence, hunters who handle them are at particular risk. Despite the existence in modern times of antibiotics such as streptomycin and vaccines, there were 500 recorded cases of plague in the Vietnam conflict (1965–1973), and over 1500 fatalities have occurred in developing countries since then. Plague outbreaks have occurred in India (1990s), Uganda (2000) and in Gansu, north-west China (2014). Although other microbes have been implicated in historical episodes of 'plague', including influenza and Ebola (Holden, 1996), the progress of the disease with an initial massive impact followed by recurrent localized episodes, plus the characteristic symptoms of the bubonic form, make this doubtful.

Clinically, there are bubonic, septicaemic, pneumonic and rarely meningeal forms of plague. The first two are transmitted classically by fleas associated with murid rodents and the third by breathing in water droplets coughed out by an infected person. The pneumonic form may have been more prevalent in cold conditions, when people sought the cloistered warmth of their dwellings. This and the septicaemic form kill almost everyone they infect. The bubonic form kills about half of young, healthy adults, more of the old and very young, and is identified by swellings (buboes) near the groin and/or armpit, close to the lymphatic nodes. Apart from rats, other reservoirs of infection included mice and domesticated and feral cats and dogs in urban areas, some of which were buried along with people in the mass graves. Today in rural areas, squirrels, field rodents and rabbits are often involved in the spread of sylvatic plague. In Central Asia from Kazakhstan to Mongolia (40°–50°N) foci of plague exist in a variety of rodents including the gerbils (*Rhombomys opimus, Meriones meridianus*), and the little suslik (*Spermophilus pygmaeus*), being spread by various fleas. Such an ecological complex, in which a disease of animals is transmissible to us, is called a *zoonosis*. This is an anthropocentric term in which we are to give ourselves pride of place. In a rat's view we would be part of the zoonosis, one particularly dangerous because of our global mobility! Indeed, plague has spread classically along trade routes. Diseases such as malaria, that involve only insects and people, are called *anthroponoses*: we are the principal host although the insect vectors may also suffer.

There is a story, ecologically neat but possibly erroneous: in the late seventeenth century Europe, the domestic black rat *Rattus rattus* and flea vector *Xenopsylla cheopis* (Fig. 7.2) were displaced by a southward migration of the big brown rat *Rattus norvegicus*. Black rats took refuge in roofs. This shift of abode was sufficient to remove *X. cheopis* from our proximity, reducing the chance of infection. At any rate, there has been no European pandemic since that time, but *X. cheopis* is presently found on both rat species, so that the reality is not as simple as the story, as is often the case. Since several genera of fleas are now known to transmit plague it seems likely that other fleas, including *Pulex irritans* and cat and dog fleas, were involved in the spread of the Black Death, although now inefficient vectors. Also, it is likely that plague declined because the human survivors and their descendants had enhanced resistance to it, while persons who were not resistant were too sparse to maintain its dynamics. Supporting this, the re-occurrence of plague in Marseilles in 1722 killed few people, which may be a telling example of the power of natural selection in a human population.

We note that domestic hygiene at this time was unknown. All manner of discarded waste was trodden into the rush-strewn floors, providing both food and nesting materials for rats and other resources for flea larvae. Most people were flea bitten daily. (That familiarity with insect vermin can breed contempt for them is shown in the photograph of a young Masai lady, oblivious of her visiting *Musca sorbens*.) As in the case of malaria, foul smells (miasmas) were thought to be the cause of the disease and plague doctors wore capes and head gear to protect themselves, breathing through beak-like respirators filled with bouquets (Fig. 7.3).

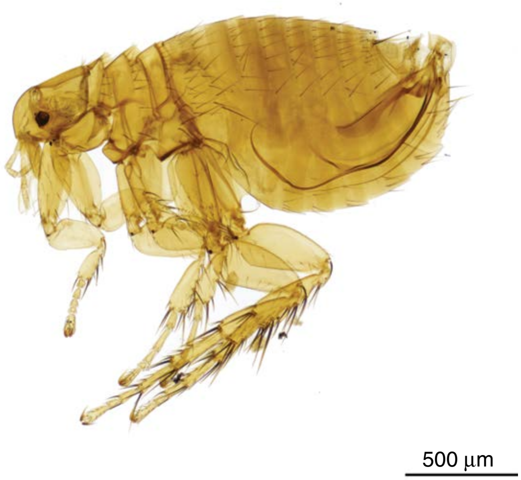


Fig. 7.2. Adult of the flea, *Xenopsylla cheopis* (Siphonaptera), one of several fleas capable of transmitting the coccobacillus *Yersinia* which causes plague. Source: Wikimedia Commons, author Olha Schedrina / The Natural History Museum.

Although several species of fleas can transmit plague they vary greatly in their efficiency as vectors. This is associated not only with the likelihood of their biting people but also with the concentration of plague bacilli that develops in their guts: high numbers of these bacteria making an individual flea more infectious. Multiplication of the bacillus can cause blockage of its gut, and the flea regurgitates them onto its host. In addition, a 'blocked' flea becomes desiccated and hence tries to feed insistently. In this connection hot, dry weather soon kills fleas searching for a sanguineous meal, so that plague does not spread so easily under these conditions. Both the flea's mouthparts and its faeces are infective; the latter (like louse and triatomine faeces) may be scratched into a bite, puncture or abrasion. Moreover, flea faeces may remain infective for three years.

Xenopsylla cheopis was first described (as *Pulex cheopis*) from a variety of rodents along the River Nile (Rothschild, 1903). While unsuspected as a plague vector then, it is the main source in the Indian sub-continent. Although *X. astia* is common on rats there, it bites people less frequently. *Xenopsylla brasiliensis* is common not only in South America, but also in Africa and India and is an efficient vector. *Xenopsylla astia* is found in South-East Asia and *X. vexabilis* in Australia. Two other fleas, *Nosopsylla fasciatus* and *Leptopsylla aethiopica* may also transmit plague. Black rats are very susceptible to the disease, and when infected may be distinguished by their fearless and erratic behaviour. Typically, adult fleas leave a moribund host and then become an infective agent to us. Plague bacilli do not reach such high numbers in the guts of other fleas, including *Pulex irritans*. Domesticated dogs are susceptible to plague, but horses are apparently immune, which is fortunate since the morbid task of hauling human corpses to mass graves fell to our four-footed friend. When treating a focus of plague, one must kill both the rats (bromadiolone, chlorophacinone) and the

Fig. 7.3. A plague doctor's outfit from the time of the Black Death. The beak was filled with fragrant flowers to obliterate bad smells (miasmas) then, as with malaria, thought to cause the disease. Source: Wikimedia Commons, The Wellcome Trust.

escaping fleas (carbaryl, fumigation with permethrin or pirimiphos methyl) or parasitic transmission may continue.

7.2.2.2(c) OTHER FLEAS. Apart from their association with plague, dog and cat fleas (*Ctenocephalides canis* and *C. felis*) are involved in the transmission of the tapeworm *Dipylidium caninum* to ourselves and particularly to our infants, often when they are less than 6 months old. The dog louse, *Trichodectes caninum*, can also act in this way. The eggs of the adult tapeworm are passed in faeces, ingested by a larval flea, and retained as a cysticercoid within the adult. Children are often mistakenly allowed to kiss and cuddle pet dogs and cats, so it occasionally happens that they swallow a flea. These pets more frequently ingest these fleas when they groom themselves, but the tapeworm, apart from living in the guts of cats and dogs, seems to have adapted to its human domesticator (Diamond, 1999). When these pets are allowed into the house they must be de-fleaed and de-wormed regularly. Due to central heating, fleas on household pets are increasing in numbers in temperate regions (Hill, 1997). Preparations containing insect growth regulators (Section **13.2.3.2**) are particularly effective against such beasts and can be applied conveniently as a flea collar or in the pet's food.

Tunga penetrans, popularly known as the sand flea, jigger, chigger or chigoe, is an aberrant species found in tropical Central and South America, its original home, but was introduced to Africa at the end of the nineteenth century. Larval development occurs in dry, sandy soil and adult females penetrate human toes, particularly under the nails, but other regions such as the groin, elbows and hands can be infected. The embedded flea swells to the size of a small pea and may eject several thousand eggs. The feet of domesticated mammals, particularly pigs, but also cats and dogs, may be attacked, thus providing a reservoir population (Section **13.1.2.2**). The combination of sandy soil, primitive housing and children running barefoot amidst unrestrained animals, is a common sight in the areas listed above; one in which jiggers thrive, and their unhygienic removal can lead to septicaemia and even tetanus. They also transmit the *Rickettsia* causing scrub typhus (Traub and Wisseman, 1974). Since the late 1980s, ivermectins have been used to treat infection by this pest.

7.3 Micropredators

7.3.1 Exopterygota: Hemipteran micropredators

These do not have the extensive mobility and flight control of their dipteran counterparts shortly to be considered. Both adults and large nymphs attack at night, crawling onto their victim and sucking blood. But in common with ectoparasites, they transmit pathogenic micro-organisms via faecal contamination.

7.3.1.1(a) HETEROPTERA; Reduviidae, Triatominae. *Triatoma*, *Rhodnius*, *Panstrongylus*, *Eratyrus*. Multiplicative vectors of Chagas' disease in the

New World tropics and sub-tropics. The Reduviidae form a large family of predatory bugs most of which eat other insects (Section **8.2.2.3(c)**). A few big ones (Fig. 7.4), however, sometimes separated in the Triatomidae, while not being very specific, suck the blood of tetrapods, including people, and depart. They are long lived: development through five nymphal instars may take as long as a year and adults may live for a similar period. Fecundity reaches several hundred eggs per female if food is adequate. Most adults fly readily, often redistributing themselves during the rainy season.

Over extensive rural and in diverse urban areas of tropical South and Central America, people often live in sub-standard dwellings. One frequent type is wattle and daub, a form of building used in Europe until, during the Industrial Revolution, it began to be replaced by brick. In this traditional construction a wooden framework with a finishing layer of lathes is daubed with mud or clay. In the Neotropics, triatomine bugs frequently inhabit spaces within the walls, which develop as the wood dries and rots. They tend to pass the heat of the day in the upper part of the walls, where the palm thatch shades them (Schofield, 1979; Weeks and Cordon-Rosales, 2013). One house investigated was home to over 8000 of the brutes. Their presence in numbers is readily detected as they leave black and white faecal marks, not to be confused with those of lizards, on the walls. Upgraded housing, using composition block walls, filled, rendered and painted, is an ideal solution. The replacement of thatched roofing by galvanized or aluminium sheeting is also helpful, but anyone who has experienced the elevated temperatures in such houses would plead for the return of thermally friendly thatch, bugs and all. Even so, thatch can be used above the sheeting purely as insulation. Significantly, palm leaves frequently transport triatomine eggs, as those of some species are cemented to them (Gamboa, 1973a, in Schofield, 1979). While costs of restructuring are far greater than those of spraying, houses are permanently improved and have added value. The cheapest method of control (~US$30/house) is to spray the interior walls of dwellings on an annual basis; but many things, apart from diseases, move slowly in the tropics. HCH, the traditional insecticide of choice, has been replaced by pyrethroids such as deltamethrin (Decis), cyfluthrin, cypermethrin (Ambush) and lambda-cyhalothrin (Icon; Section **13.2.3.2**). Insecticidal paints containing fenitrothion and yeast-baited traps have been used.

Fig. 7.4. Adult of a triatomine bug (*Triatoma*), a vector of *Trypanosoma cruzi* the causal organism of Chagas' disease. Source: Wikimedia Commons, author Felipe Guhl.

These bugs also associate with livestock, especially chickens, and may rest during the day in the ramshackle dwellings often provided for them, so forming reservoir populations (Section **13.1.2.2**), and a source of re-infection. They also seek rodent burrows, especially in Central America, and in Panama and probably elsewhere they have retreats in palms that retain their leaf bases. Their natural enemies are poorly known, but in domestic situations fowls are major predators, followed by wood rats and lizards. Many species possess defensive 'Brindley's' glands in the metathorax. These secrete isobutyric acid. Ants attack the egg batches, which are also parasitized by the wasp *Gryon*. As in gypsy moths (Section **5.2.1.4(f)**), peripheral eggs are more vulnerable.

At night these bugs leave their hideaways and bite sleeping persons, particularly on the face and around the mouth, engendering the endearing name 'kissing bugs'. Like mosquitoes and tsetse they respond to elevated CO_2 levels, but also to ammonia. Probably to speed up feeding, during which they are vulnerable, *Rhodnius*, and no doubt other genera, inject a vasodilator into their host. More importantly, they spread the protist *Trypanosoma cruzi*, the causal organism of Chagas' disease, named after the Brazilian biologist Carlos Chagas, who discovered it in 1909. This microbe, like

Leishmania (Section **7.3.2.4**) and *Phytomonas* (Section **5.3**), belongs to the Sarcomastigophora. Some 70 species of triatomine bugs harbour *T. cruzi*, but fewer transmit it to people. They have the unprepossessing habit of defecating while feeding, adding insult to injury, but allowing room for a little more food. Indeed, they often suck up more than their own initial weight of blood. But the possibility that this is due to manipulation by *T. cruzi* should be considered (cf. *Leishmania*). The infective stages of the trypanosome, or trypomastigotes, contained in the faeces then enter the wound (Brumpt, 1912), by being scratched into the puncture during a troubled sleep, although often they enter through the conjunctiva of the eye. Bites near an eye cause the lid to turn purplish and swell, an early symptom known as Romana's sign. Infection may also occur by eating food contaminated with their faeces, or by eating under-cooked, infected opossums. These bugs are efficient vectors because they are long lived in relation to the life cycle of their resident trypanosomes, unlike most mosquitoes and sand flies whose life expectancy is relatively short (Section **13.4.1**).

After an initial acute infection, in which the trypanosomes attack the macrophages of the blood, they eventually pass to the heart, penetrating the cardiac muscle and taking up shop, although other tissues may be affected. If treated early the disease can be cured with benznitazole or nifurtimox. Later there may be a massive distension of the oesophagus and colon, thought to be an autoimmune response (Cox, 2002). Slow degeneration of the heart ensues until it ceases to function, a decline often taking several years. Ultimately, as much as 80% of the cardiac tissue may be destroyed. The disease can also be transmitted in blood transfusions that have not been properly screened for pathogens and from mother to child, namely *vertical transmission*, the latter being the major pathway (Gurtler *et al*., 2003).

At present, there are >120 million persons at risk, a figure that has been rising due to a rapid increase of the human population in the region affected. Despite this, the number of sufferers has been falling from ~17 million in 2002 to only ~ 6–7 million in 2017. The number of annual deaths has been reduced from ~21,000 in 2002 to ~12,000 in 2017. It was suggested that Charles Darwin's poor health and his demise in 1882 were results of his contracting Chagas' disease during his South American travels in 1835, and he even describes being attacked by *Reduvius*. Although he had chronic heart and other health problems during his life, death would normally result more speedily. In addition, some of his afflictions preceded the trip (Medawar, 1967).

Different triatomine species more commonly transmit the disease in different parts of its patchy distribution. This extends from a little beyond the tropics in northern Mexico and Texas in the Corpus Christi region, where *Triatoma rubrofasciata* is found, to northern Argentina. But occasionally these bugs occur south of the Rio de la Plata. *Triatoma dimidiata* is found in most of Central America, *T. barberi* in Mexico, *T. infestans* in Chile, Argentina and southern Brazil, *Rhodnius prolixus* in northern Brazil, *Panstrongylus megistus* in southern Brazil, Trinidad and Venezuela, and *Eratyrus cuspidatus* in Panama. In Central America, up to 30% of the bugs carry *Trypanosoma cruzi*, but in Brazil the figure is only ~5%. But these are relatively high levels of infection (see Section **7.3.2.4(b)**). The protist is also found in the great variety of wild and domesticated mammals that triatomines bite, but particularly dogs and opossums, forming a reservoir of potential human infection. Hence, like plague (Section **7.2.2.2(b)**), there is a *zoonosis*. The bugs also bite each other, so becoming infected by another route of vertical transmission (Section **7.3.2.4(b)**). There are occasional records of triatomine bugs transmitting other human diseases, for example murine typhus and equine encephalitis. They also commonly spread *Trypanosoma rangeli*, which is ostensibly asymptomatic. *Trypanosoma cruzi* itself, which has not been formally divided into sub-species, is more virulent in Venezuela than in Brazil and the USA (Ewald, 1983).

7.3.1.2(a) HETEROPTERA; Cimicidae. *Cimex lectularius* and *C. hemipterus*. Bed bugs. Tropical and sub-tropical nuisance biters. Some species are avian ectoparasites. *Cimex lectularius* is almost cosmopolitan in warm regions while *C. hemipterus* is pan-tropical. These bugs are flightless, oval in shape and ~5 mm long. Like triatomines they shelter by day in crevices in human dwellings and both sexes bite sleeping people at night. They also leave faecal stains on walls and bed sheets. Their attacks may be so severe as to cause anaemia in young children. Like many haematophagous insects they harbour microbial symbionts. Despite the fact they carry pathogens, these are not known to replicate within them, nor do they transmit any disease to man (Reinhardt and Siva-Jothy, 2007). Cimicid bugs also associate with birds, particularly swallows and martins, and *Leptocimex boueti* with bats. There is resurgence of these cryptic beasts in recent years and in Australia and North America trained sniffer dogs have been used to detect them.

7.3.2 Endopterygota

7.3.2.1 General introduction

The only order of importance here is the Diptera. Although it is the highly mobile adults that bite, these pests are often best kept in check by modifying larval habitats. Some species of mosquitoes rest indoors and are termed '*endophilic*', contrasting them with the '*exophilic*' habits of the majority. Some of the latter group, however, bite indoors (*endophagic*). Endophilic insects are obviously easier to control, but due to house spraying some have now evolved exophilic habits (Pates and Curtis, 2005). On the Kenyan coast, endophilic *Anopheles gambiae* s.l. and *An. funestus* are aggregated, with >90% of these mosquitoes collected from <50% of houses (Keating *et al*., 2005). Such clumped populations pose added problems for accurate sampling (Section **9.3**).

7.3.2.2 Diptera: General

Before considering further examples in this section, we list (Table 7.1) the many dipteran genera containing pest species, emphasizing their cardinal role in both medical and veterinary entomology. As we noted (Section **7.1**) micro-organisms have evolved to exploit the effective host-seeking abilities of these vectors.

7.3.2.3 Dipteran mouthparts

Since most dipteran micropredators are equipped with piercing and sucking mouthparts it is helpful to explain the basic principle of such organ systems, the mechanisms throughout being broadly similar. The labium forms the bulk of the structure, but there are differences in detail. In the biting Nematocera and Brachycera, the labium does not pierce but forms a ventral, gutter-like sheath to the piercing and sucking elements, which have evolved from the mandibles, maxillae (paired) and hypopharynx (single). The latter structure normally conveys saliva containing an anticoagulant into the host, fluids that are produced by salivary glands associated with the labium. A variously formed channel conveys the blood into the insect, assisted by an alimentary pump, the cibarium. The mandibular stylets do the piercing in all primitive genera, assisted by the laciniae (the sharp parts of the maxillae) and hypopharynx in mosquitoes, but only by the laciniae in tabanid flies. In *Simulium* and *Culicoides,* however, the mouthparts are short and have a rasping action and, as in tabanid flies and the biting muscids, blood is lapped up by the labium after an initial puncture, a method known as pool feeding. In tabanid flies the mouthparts are a veritable stabbing organ, inflicting severe, deep bites, the blood being mopped up by the labellae. In biting muscid flies, the labium itself is intimately associated with other mouthparts to form a

Table 7.1. Dipteran genera involved in disease transmission that have piercing mouthparts (*) and those causing myiasis ($^{\mathrm{m}}$).

Sub-order: NEMATOCERA		
	Phlebotomidae*...........	*Phlebotomus, Lutzomyia, Sergentomyia*
	Culicidae*.............	*Anopheles*, *Culex*, *Aedes*, *Haemagogus, Sabethes, Mansonia Psorophora*
	Simuliidae*.............	*Simulium, Prosimulium, Cnephia*
	Ceratopogonidae*.......	*Culicoides*, *Leptoconops*
Sub-order: BRACHYCERA		
	Tabanidae*.............	*Tabanus*, *Chrysops*, *Haematopota, Hybomitra, Lepiselaga*
Sub-order: CYCLORRHAPHA		
	Oestridae$^{\mathrm{m}}$.............	*Oestrus*, *Rhinoestrus, Cephalopina, Hypoderma*, *Gasterophilus*, *Dermatobia*
	Calliphoridae$^{\mathrm{m}}$.........	*Lucilia*, *Calliphora*, *Cochliomyia, Auchmeromyia, Cordylobia, Wohlfahrtia*
	Muscidae.............	*Musca,*$^{\mathrm{m}}$ *Muscina,*$^{\mathrm{m}}$ *Fannia,*$^{\mathrm{m}}$ *Glossina,** *Stomoxys,** *Lyperosia,** *Haematobia**

proboscis, which is the organ of penetration. Except in the latter group it is only the females that bite, an example of Kipling's Rule that the '… female of the species is more deadly than the male'!

On the face of it, sucking blood from a tetrapod is fraught with difficulties for a micropredator. The host's reactions to wounding include haemostasis, inflammation and immunity, which must be combated. Ribeiro and Francischetti (2003) discuss the ways in which the complex and variable 'salivary cocktail' enables the micropredator to do this. It contains various anticoagulant and vasodilatory substances. Agents suppressing the human immune system have been suggested. It is probable, too, that pain killers are present (Waage, 1979; Service, 2000), particularly in insects like triatomine bugs that must feed for an extended period, since in primates at least the pain of penetration would result in the little assailant being swatted.

Blood sucking allows females to acquire food of relatively high quality to metabolize, to promote oogenesis and enhance fecundity. So we can surmise the evolutionary forces shaping their behaviour. Very often biting flies in the Nematocera and the Brachycera breed in environments poor in nutrients. These include natural situations on acid moors and bogs of north temperate climes, in temporary water in rot holes in trees, in small pools in limestone, in cut bamboo, in tropical bromeliads and in large fallen leaves such as those of the Neotropical tree *Cecropia*. They also use wet, nutrient-deficient soils in tropical rain forests. This extensive environment, together with moorland, provides diffuse habitats that are difficult for us to alter and effect economic control. With more discrete habitats, that are a result of human activity, control is potentially easier: it just needs a little thought. These sites include water bodies such as paddy fields, irrigation systems and surface water associated with construction sites, and also a variety of human rubbish (Section **7.3.2.4(c)**).

Where the families are of sufficient importance we will give a brief general section on their biology.

7.3.2.4 Dipteran micropredators

7.3.2.4(a) DIPTERA; NEMATOCERA; Phlebotomidae. *Phlebotomus, Lutzomyia, Psychodopygus*. Sand flies. Cosmopolitan biters and disease vectors afflicting people and other mammals. This family, which was split from the Psychodidae some years ago, comprises ~700 species and six genera, but there are only three genera with females that bite people. Old World *Phlebotomus* and New World *Lutzomyia* carry the protistan parasites *Leishmania* spp., which are distant relatives of trypanosomes, and generally form zoonoses. They also carry lizard malaria (Fialho and Schall, 1995), while *Phlebotomus* may carry pathogenic viruses. *Lutzomyia verrucarum* carries *Bartonella bacilliformis* causing Oroya fever (Bartonellosis) in the high Andes. The third genus, *Sergentomyia*, found in parts of the Old World tropics, bites people but is not a vector.

Minute eggs are laid in batches of 30–70, according to species, in diverse damp situations. The scavenging larvae, which have a complete head capsule like most other nematoceran larvae, are characterized by four long caudal setae and tiny 'matchstick' hairs on the body. Larval development is surprisingly slow. Thus, the complete life cycle of *Phlebotomus longipes* in Ethiopia at 20°C was ~100 days, reducing to only ~50 days at 28°C. This is in marked contrast to tropical mosquitoes, which often have life cycles of <2 weeks. In temperate and arid regions the final, fourth larval instar may undergo diapause. The pupa, which generally lasts ~1 week, retains the larval skin, with its characteristic setae, attached posteriorly. But juvenile stages are seldom found. Many New World species may breed in organically rich media and contaminated soils associated with mammalian and human shelters, although *P. celiae* has been found in termite mounds in Kenya. Sand flies bite at night or at dusk and rest during the day. They need nectar for maintenance and for the development of *Leishmania*. Adults shelter in hollow trees, between tree buttresses and in dense foliage in humid forests, but in animal burrows, termite nests and crevices in the soil or rocks in more arid environments. The number of species given below is far from exhaustive but provides students with some idea of the complexity of the situation.

7.3.2.4(b) PHLEBOTOMID FLIES AND DISEASE. Phlebotomid flies transmit two different groups of human diseases.

Viral sand fly fever. Firstly, 'Pappataci' or 'three-day fever' was one of the earliest diseases shown to be transmitted by an insect, when Doerr *et al.* (1909) demonstrated this for *Phlebotomus papatasi* (Fig. 7.5) in Herzegovina. The disease is now centred in the south of the Palaearctic Region, where the flies may breed in and around primitive dwellings, but extends to the Mediterranean islands, the Nile Valley, India and Bangladesh. Three-day fever is a misnomer, since episodes may last up to 2 weeks. While debilitating, it is fatal only when the sufferer is very poorly fed. It is often variously misdiagnosed as influenza, dengue fever and even malaria. The eggs of an infected female may also carry the virus, which may hence be vertically transmitted to surviving adult progeny.

Leishmaniasis: General. This second group of diseases is a complex of three basic types and in total there are < 1 million new cases and 20,000–30,000 deaths annually. Complexity is due partly to there being several species of *Leishmania* affecting various regions of the body, but also because what is ostensibly the same species of *Leishmania* may cause different diseases in different places. While there are exceptions, in the Old World these diseases are mainly found in savannahs, while in the New World they are usually caught in forests (Lainson, 1983). But the larval environments of phlebotomine flies are poorly known (Feliciangeli, 2004). Globally, the various forms of leishmaniasis affect ~12 million people (Desjeux and Alvar, 2003). However, although leishmaniasis and its vectors are complex, its impact on human life is far less serious than malaria (Section **7.3.2.4(d)**).

Visceral leishmaniasis (VL).

The potentially fatal disease *kala-azar*, or 'black sickness', is caused by the *Leishmania donovani* complex, *Le. donovani* and *Le. infantum,* and *Le. tropica* in the Old World and by *Le. amazonensis* and *Le. chagasi* in the New World. There are presently 200,000–400,000 new cases annually, and if untreated the disease is normally fatal within 2 years, but many healthy people are wholly or partly resistant. The parasites invade several regions of the body, this being dependent on where the vector bites, but frequently the spleen and liver become seriously infected, and anaemia ensues. They are transmitted by several *Phlebotomus* species in three, mainly arid regions: (i) India and Bangladesh; (ii) Sudan, South Sudan and Ethiopia; and (iii) Brazil. The vectors include *Phlebotomus perniciosus, P. longicuspus*, *P. major, P. simici*, *P. chinensis, P. duboscqi*, *P. argentipes* and *P. langeroni*. In these regions *Leishmania* may also be present in wild and domesticated dogs and some rodents including porcupines, thus forming a zoonosis, but the composition of this reservoir of parasites varies considerably from place to place.

Fig. 7.5. *Phlebotomus papatasi* (Phlebotomidae), an Old World sand fly that can transmit the virus causing three-day fever. This disease was one of the first shown to have an insect vector (1909). Source: Wikimedia Commons, Centers for Disease Control and Prevention's Public Health Image Library.

Le. infantum, as its name suggests, affects mainly children but also dogs. It is distributed along the whole Mediterranean littoral, but more frequently in the west. Recently, the number of cases in patients immunosuppressed by HIV has increased. Such persons are more likely to develop VL from a *Leishmania* infection (Desjeux and Alvar, 2003). But in Europe at least, therapy has reversed this trend. In the New World tropics and sub-tropics, transmission is by the *Lutzomyia longipalpis* complex, among other phlebotomid species.

Cutaneous leishmaniasis (CL)

In the Old World, *Leishmania tropica*, *Le. major* and *Le. arabica* species complexes are transmitted by numerous species of *Phlebotomus*, including *P. perniciosus*, *P. longicuspus*, *P. major*, *P. martini*, *P. ansarii*, and *P. sargenti*, causing various disfiguring, cutaneous sores such as Oriental sore, Aleppo button and Delhi boil. Most of the cases (0.7–1.3 million annually) are in tropical or Mediterranean situations but particularly in Algeria, Syria, Iran and Afghanistan, and also in Brazil and Colombia. Again, in parts of southern Europe the crippling effect of HIV on the human immune system has recently led to subclinical cases of this leishmaniasis becoming overt. In the New World, the *Le. mexicana* and *Le. brasiliensis* species complexes may cause cutaneous as well as mucocutaneous infections.

Mucocutaneous leishmaniasis (MCL).
This disease is caused by any of several *Leishmania* species that attack the lymphoid macrophages in superficial regions of the body, particularly the oral and nasal cavities. In the New World it is confined to tropical and sub-tropical South America, especially north-east Brazil, Surinam and the Amazon Basin, where it is called *espundia*, parts of Central America and also Bolivia and Peru. It is much more frequent in people working in densely forested regions. It can be extremely disfiguring in chronic cases, for example in those *materos* (backwoodsmen) who have been untreated, much of the nose and lips may be eroded. The major species complexes involved are *Leishmania braziliensis*, *Le. guyanensis* and *Le. mexicana*. The vectors are *Lutzomyia* and *Psychodopygus* (both formerly in the genus *Phlebotomus*). A very large number of vectorial species are involved and are found in different geographical regions. We mention only a few:

- Brazil: *Lu. longipalpis*, *Lu. olmeca*, and *Lu. whitmani*, *Ps. wellcomei*;
- Colombia: *Lu. spinicrassa*, *Lu. trapidoi*;
- Venezuela: *Lu. migonei*, *Lu. gomezei*; and
- Mexico: *Lu. olmeca*, *Lu. diabolica*.

In the New World several mammals (domesticated and feral dogs, donkeys, a variety of wild rodents and small marsupials) also carry *Leishmania* so that, as in Chagas' disease, there is a complex zoonosis.

There is evidence that *Leishmania*, despite their supposedly lowly position on the evolutionary scale, have evolved to manipulate their more sophisticated insect vectors (see Section **7.3.2.2**). Thus, *Lutzomyia longipalpis* carrying *Le. mexicana* take smaller, more frequent meals than uninfected flies, so increasing the chance of transmitting the parasite (Rogers *et al.*, 2002). This recalls essentially comparable situations: first, that in which *Yersinia pestis* blocks the gut of its flea vectors (Section **7.2.2.2(b)**) and second, that of the myxoma virus (Section **7.3.4.2(f)**) becoming less virulent to rabbits, both strategies potentially enhancing pathogenic transmission.

In the Amazon Basin the proportion of potential vectors that is infected is small, often less than 1% (Lainson, personal communication, 1967) so that one can get a lot of bites before getting the disease. Such rarity recalls the situation in Brugian and Bancroftian filariasis and in sleeping sickness (Sections **7.3.2.4.(g)** and **7.3.2.4(n)**, respectively). It also makes the vectors difficult to study scientifically. Within this vast region transportation is largely by light plane or by river, and despite the building of the Transamazonica, there are still huge tracts of impenetrable forest. One appreciates that the natural complex of protistan parasites, vectors and secondary mammalian hosts cannot be eradicated. Hence, efforts must be directed towards avoiding being bitten, and improving prophylactics and cures. At present the development of vaccines is underway. It was estimated in 1995 that although 370 million people were at risk in the New World, there were only half a million cases annually. This is probably because, with the exception of *Lu. longipalpis* s.l., most of the vectors stay near undisturbed forest. In the Old World mucocutaneous leishmaniasis is not so extensive, but clinically similar cases are found in Ethiopia and the Sudan, where they may be caused by *Le. tropica* and *Le. major*. Fairly recently, *Wolbachia* (Sections **10.2.3.9** and **13.2.2.2**) has been found in *Phlebotomus papatasi* and *P. perniciosus*. This α-proteobacterium may be useful in driving transgenes into these vectors as a means of control (Benlarbi and Ready, 2003).

7.3.2.4(c) DIPTERA; NEMATOCERA; Culicidae.

Mosquitoes. Cosmopolitan nuisance biters; major disease vectors in warm countries. Mosquitoes are by far the most important family of insects that transmit human diseases. These amount annually to some 450 million new cases of malaria, filariasis and various viral infections and 3–4 million deaths, the majority in sub-Saharan Africa. Before their vectorial capabilities were known, their spreading malaria and yellow fever was the major cause of the French failing to complete the Panama Canal in the late nineteenth century. In all, an estimated 48,000 workers died of yellow fever alone before the canal was finished. Of course, mosquitoes are irritating nuisance biters, reducing the efficiency of our work, whether manual or cerebral. There are three sub-families: the Anophelinae, the Culicinae and the Toxorhynchitinae, together comprising ~3000 species and sub-species and 37 genera (Service, 2000). Like aphids, a small family with a big impact.

The juveniles flourish in diverse aquatic environments, including the edges of slow flowing waters, small ponds, temporary pools, rain-filled tyre tracks, water contained in rot holes in trees and in Neotropical bromeliads. Because we modify our water resources in so many ways, but especially in agriculture (Pennisi, 2001), mosquitoes typically associate with us. We often inadvertently increase the density and quality of their breeding sites (patches; Section **12.3.4.4(g)**). In Michigan, USA, when urban wastewater was disposed of into a 200 ha marsh, the populations of several local mosquitoes were increased (Zaim and Newson, 1980). Other man-made sites are rice paddies and irrigation channels, pools on construction sites, cut bamboo and a variety of human rubbish, especially discarded worn-out tyres, water storage pots and the tubs of washing machines, which when made of stainless steel never rot away. The global trade in used tyres is the probable cause of the spread of *Aedes albopictus* into the southern USA, a species that also breeds in flower vases in cemeteries. In sum, mosquitoes cause us a great deal of trouble. This is reflected in the fact that *their* population densities relate to the same spatial scale as *ours*. We will see (Section **12.3.4.4**), however, that the nature and change of their spatial environment is a major determinant of these densities relative to that of the human one affected.

The adults are all too familiar and quickly separated from several genera of small Tipulidae, which are of rather similar shape, by their elongated proboscides and because their wing veins, thorax, abdomen and legs bear scales. The Anophelinae contains the genus *Anopheles* with ~430 species. The Culicinae has all the other genera important as vectors. The Toxorhynchitinae are big, often dark metallic blue, have a recurved proboscis, and do not bite people. The >70 species are mainly tropical and have larvae that eat all sorts of mosquito larvae. Malarial transmission is confined to ~70 species of *Anopheles*, but culicine mosquitoes spread a wide spectrum of other diseases. Unlike most mosquitoes, adult *Anopheles* rest with their heads down and their backsides up, while their wing veins often bear patches of black and white scales (Service, 2000). The females have palps about as long as the proboscis, while in culicine mosquitoes they are shorter. As in several other Nematocera (Section **10.2.5.1**), males may form crepuscular swarms.

Generally, female *Anopheles* lay single, boat-shaped eggs with lateral floats on the surface of various, *permanent* water masses. Atypically, they oviposit in *temporary* patches such as puddles or, like *An. bellator* and *An. cruzii,* in water in bromeliads. Their eggs desiccate easily. About 15 malarial species breed in rice paddies (Mogi, 1984). Most mosquito larvae filter-feed but also crush up larger organic particles in their mandibles. *Anopheles* larvae generally feed near the surface. They breathe through paired dorsal spiracles in a hydrofuge area at the end of the abdomen. Mosquito pupae are comma shaped, have short, respiratory thoracic 'trumpets' and are actively mobile. In most genera both the larvae and pupae breathe air from the water surface, scurrying downwards if disturbed. But in *Mansonia* and *Coquillettidia,* both these stages pierce the stems of aquatic plants to obtain air and so are restricted to weedy environments. Adult *Anopheles* bite at night or in the evening, either indoors or outdoors according to species (Pates and Curtis, 2005).

The Culicinae, with some 2700 world species, contains the medically important genera *Aedes*, *Psorophora, Culex, Mansonia, Haemagogus* and *Sabethes*. *Aedes* and *Psorophora* lay single eggs, *Culex* lays them in cohesive rafts, and *Mansonia* deposits them in gelatinous masses on the underside of aquatic leaves. Culicine eggs never have floats. *Aedes* and *Psorophora* often lay in places likely to hold water after rain, indeed the eggs must be wetted before they hatch. Often only a few eggs hatch after the first wetting, several inundations being required for all to hatch, another example of risk spreading (Section **9.7**). Even so, eggs may die from desiccation, small ones with their higher surface to volume ratio being more vulnerable. *Aedes aegypti* and to a lesser extent *A. albopictus* have relatively large, drought-resistant eggs (Soto and Mogi, 1992). Hatching in water may also be inhibited by the presence of numerous conspecific larvae, and larval competition for space (Section **9.8**) is common in *Aedes* (Juliano, 1998). It is mediated by chemical or physical interference and even results in cannibalism (Broadie and Bradshaw, 1991). Culicine larvae, excluding *Mansonia* and *Coquillettidia*, have long posterior, respiratory siphons, by which they hang from the surface film, typically at an angle of ~45°.

In Central and South America, adult *Haemagogus* and *Sabethes* have red, green, gold or blue metallic scales on their bodies (Fig. 7.6). These colours recall those of several insects that are active in sunshine (blow flies, many dolichopodid flies, some euglossine bees) and may well have a thermoregulatory function (Section **10.2.4.2**; Willmer, 1982). We are unsurprised, then, that these mosquitoes bite mainly in the forest canopy during the day. Additionally, the colours and patterns might possibly be used to recognize conspecific mates, as may the ornamented legs in *Sabethes*. Such adornments are also common in dolichopodid flies (Section **8.2.2.4(h)**).

Fig. 7.6. Adult *Sabethes* (Culicidae) showing coloured wing scales and leg adornments.

Tropical mosquitoes often have high death rates, short life cycles and high fecundities, driving rapid fluctuations in their populations. Many are also very mobile and hence are extreme *r*-strategists (Section **9.1**). Autogenous mosquitoes, like *Culex molestus*, produce some eggs without a blood meal but many more when fed. Anautogenous species, like some *C. pipiens* (Section **7.3.2.4(f)**), need a blood meal in order to lay eggs and some *Anopheles* must have two such meals (Dye, 1992). Some species also suck caterpillar haemolymph, augmenting egg production (Harris *et al.*, 1969). Egg laying commences ~3 days after feeding, and, according to species and size, 30–300 eggs are laid. Females replete with blood, as one would suspect, are at greater risk from predation, particularly from spiders (Roitberg *et al.*, 2003). Mosquito-borne diseases spread rapidly in rainy seasons. In Ethiopia in 1958, heavy rains resulted in dense populations of *Anopheles arabiensis*, >3,000,000 cases of malaria and 150,000 deaths (van Emden and Service, 2004). But in Japan, outbreaks of *Culex tritaeniorhynchus* in rice paddies, where water is not short, occur during warm, dry weather (Mogi, 1984).

The nematode worm *Romanomermis culicivorax* and even flatworms attack the larvae of some species. Numerous pathogens, but apparently no parasitoids, afflict the juveniles. *Bacillus thuringiensis* var. *israelensis* (*Bti*), formulated as a powder and sprayed onto the water surface, is generally useful and also kills larval *Simulium*. *Bacillus sphericus* is toxic to several *Culex* and *Anopheles* species, but not to *Aedes aegypti* (Kettle, 1995). *Ascogregarina taiwanensis* attacks *Ae. albopictus*, but not *Ae. aegypti*, which is more susceptible to *As. culicis* (Juliano, 1998; Section **7.3.2.4(d)**). Mosquito larvae also fall victim to protistan pathogens (*Nosema vavraia*, *Thelohania*) and to fungi (*Coelomomyces*, *Culicinomyces*, *Lagenidium*). The daily adult death rate in the field may be very high (Anderson and May, 1992), in some cases ~50%, as in *Culex tritaeniorhynchus*, the main vector of Japanese encephalitis in Japan (Mogi, 1984). Death rates in the laboratory may grossly underestimate field rates. Female *Ae. albopictus* has rates of 0.008–0.013/day in the laboratory, but only 0.11–0.20/day in the field (Chmielewski *et al.*, 2010). These translate into mean survival of 77–125 days and only 5–8 days, respectively. While mosquitoes are potentially long lived, there is massive natural attrition. Small birds, predatory Odonata, spiders, aquatic bugs such as *Notonecta* and empidid and dolichopodid flies take their toll.

Mosquitoes may fly 10 km (Johnson, 1969) or more when assisted by the wind. Several species of *Aedes* (*Ae. solicitans*, *Ae. cataphylla*, *Ae. taeniorhynchus*) can move 20 km and Glick (1939) trapped some species at heights up to 1500 m, strongly suggesting that they can move much further. An exceptional case from Australia was the arrival 100 km inland of hoards of the coastal species *Ae. vigilax*, where they bit cattle and cattlemen alike. Similar long-distance movement has been recorded for *Anopheles pharoensis* from the Nile Valley into the Western Desert (Kirkpatrick, 1957). They do, however, move much farther without a ticket in vehicles, boats (Ross, 1911) and planes. Although mainly young, unfed females actively migrate, those that have already fed, and hence potentially could transmit disease, are occasionally found to have flown a long way. Local attempts to control *Culex tritaeniorhynchus* in Japan have failed because of massive immigration (Mogi, 1984).

In Britain, only some 15% of the species do not bite us, but globally the large majority does so. Some mosquitoes are night biters, others are day biters, an activity controlled by an *internal* circadian pattern. Some species that bite us also feed on other mammals and sometimes on birds. Large mammals, such as cattle and humans, emit relatively big 'pulses' of expired, CO_2-rich air (~4.5%). Biting females respond to such CO_2 *variation* many metres away using sensitive, club-shaped receptors on their maxillary palps (Gillies, 1980; Bowen, 1991; Dekker *et al.*, 2005), but sensilla on their antennae respond to body odours such as L(+)-lactic acid and, like tsetse, to 1-octen-3-ol (Guerenstein and Hildebrand, 2008). Indeed, there is a synergistic effect within this *multi-component stimulus* (Gillies, 1980). Thus, mosquitoes do not respond to lactic acid unless a background of CO_2 variation is present. They also respond to elevated temperatures. In all, up to eight types of antennal sensilla are present (Bowen, 1991). Over 2000 neurones comprise each flagellar nerve, >90% of them serving olfactory receptors. They also possess olfactory and gustatory organs on their tarsi and maxillary palps. Day-biting species, such as *Aedes aegypti*, also employ visual cues (Kennedy, 1940, in Gillies, 1980).

People moving into mosquito-ridden regions are usually bitten much more frequently than are the locals. Our bodies manufacture natural repellents in response to bites. These compounds require the B_1 vitamin thiamine for their synthesis. A good artificial repellent is diethyl-3-methyl benzamide (DEET), which suppresses a mosquito's response to lactic acid, and may ward off attack for >6 hours. Recently, picaridin has been approved as a safer alternative and novel repellents formulated using blends of essential oils. On the other hand, mosquito populations can be sampled in traps using blends of semiochemicals (L-lactic acid, ammonia, tetradecanoic acid, 3-methyl-l-butanol and butan-l-amine; Takken *et al.*, 2015). For a popular text on mosquitoes and malaria see Litsios (1996); Clements (1992/1999) and Becker *et al.* (2010) for the heavy stuff.

7.3.2.4(d) DIPTERA; NEMATOCERA; Culicidae, Anophelinae. *Anopheles* spp. Malarial mosquitoes. Malaria is by far still the most important disease, in terms of the number of human infections and deaths, transmitted by insects. The 2016 estimates by the World Health Organization (WHO) are as follows:

- 2.4 billion persons are at risk; that is to say about 38% of the total human population.
- 370 million persons live in highly endemic regions in 90 tropical or sub-tropical countries.
- There were ~300 million clinical cases in 2002 but by 2016 this had reduced to ~216 million. In 2002 two to three million people died annually, the large majority in sub-Saharan Africa, but by 2015 mortality rate was 429,000 and 445,000 in 2016. About one-third of these deaths are pregnant women and children under 5 years old (who are often killed by severe anaemia). Malaria can also cause abortion. A high proportion of the rest is due to a cerebral form of the disease.

Apart from the unaccountable suffering malaria causes, there is a financial cost running into billions of dollars. A means of quantifying the impact of a disease to a community is the disability adjusted life year, the number of years lost due to illness and premature death. What also should be accounted is the necessary time and cost spent in caring for such patients (Hotez *et al.*, 2014). It is a necessary loss, but still a loss.

The name 'malaria' is from Latin and means 'bad air'. This name is associated with the longstanding observation that in Europe the disease was prevalent on the edges of foul-smelling marshes (marsh fever) and estuarine situations. These were, of course, the breeding grounds of anopheline mosquitoes, such as *An. atroparvus*, which we now know transmit malaria. But in the early days it was thought that dank, polluted air itself caused this affliction. This is a simple hypothesis. William of Occam (1324), proposed *essentia non sunt multiplicanda praeter necessitatem*, which is to say it is vain to do with more than can be done with fewer, a principle of parsimony known as 'Occam's Razor'. Today it means that one should test the simplest of possible hypotheses first. But it is a false hypothesis, both for malaria and plague (Section **7.2.2.2(b)**). Francis Bacon (1561–1626) warned of our habit of expecting more order in natural phenomena than is actually found, while in a rather jovial vein Turner (2000) suggested the antithesis of Occam's Razor as 'Goldberg's Lever', that true explanations are likely to be complex. Occam's Razor is a starting position, psychologically attractive rather than logically necessary (Simberloff, 1981). Importantly, Goldberg's Lever is what we generally end up with, distilled down to '*Mirationem meam nihil moveat*'… Nothing would surprise me! Parsimony may be a virtue, but not in nature. Alphonso the Wise (1221–1284) reportedly remarked 'If the Lord Almighty had consulted me before embarking on creation I should have recommended something simpler'.

Today malaria is essentially a tropical and subtropical disease, but before the twentieth century it was common in some southern European countries, especially Portugal, Italy and Greece, in the eastern USA, South-West Asia and China, often affecting agricultural workers. With global warming, should it persist (Section **2.2.2**), *Anopheles* must be expected to spread north again! Even England had a few cases, a famous one causing the death in 1658 of Oliver Cromwell. The story goes that Cromwell, the steely apex of Protestantism, in the throes of a fever refused Peruvian bark, since the Jesuits had brought it from the New World. Apart from the Huns with their advanced weaponry, malaria may have been a cause of the demise of the Roman Empire, following the expansion of marshes near Rome (see the discussion on plague in Section **7.2.2.2(b)**). During the American Civil War (1861–1865) over 50% of soldiers caught malaria and in WWI armies in Macedonia were immobilized for 3 years by it (van Emden and Service, 2004). In Vietnam, malaria was a key factor in military logistics.

About 1765 Robert Jackson, a Scots doctor practising with the British army in Jamaica and America, believed that there was a 'factor' causing malaria additional to the miasmas, a factor we now call '*Anopheles*'. He found that soldiers camped near the sea were less likely to contract the disease than those along rivers. He also showed that 'Peruvian bark' (from the tree *Cinchona pubescens*, Rubiaceae, containing quinine and long used by the Amerindians to control fevers), was effective in America, but less so in Jamaica. In the forerunner of a clinical trial he gave some troops quinine and others none (Besterman, 1988), so proving its efficacy. During the Enlightenment, Diderot (about 1774) refers to mosquitoes as ' little winged surgeons' like leeches usefully relieving us of excess blood! Of course, if the two-way passage of saliva into us and blood out of us was not suspected, so neither could disease transmission be. Only much later did Patrick Manson (1878) demonstrate the passage of filarial worms from mosquitoes to man. At that time no-one suspected the extent of this phenomenon: that *mere insects* could transmit diseases. Now, of course, we know that these may be of filarial, protistan, fungal, bacterial and viral origin, and that they can affect both animals and plants.

Fig. 7.7. Ronald Ross, the army doctor who, at the turn of the nineteenth century, discovered malarial transmission by *Anopheles* mosquitoes. Source: Wikimedia Commons.

Ronald Ross (**Fig. 7.7**), another Scots medic, mentored by Manson, attached to the British Army in India and working in the 1890s at the Sardar Patel Medical College in Rajasthan, was the first person to show insect transmission of a protistan disease such as malaria. He noted an association between the commonness of a certain 'brown', anopheline mosquito (*Anopheles culicifacies*) and the incidence of malaria in the British troops. Introducing netting for the sleeping quarters of some of the men, but not others, he showed that those protected had a lower incidence of malaria compared to those unprotected. Apparently, the troops did not mind this trial; they could not conceive that mosquitoes might carry malaria (Ross, 1911). In 1880 the French army pathologist Laveran found the protist *Plasmodium malariae* in the red blood cells of sufferers (Laveran's germ). In 1897 Ross described the development of *Plasmodium* in *Anopheles* and showed the transmission of *P. relictum* by mosquitoes to sparrows. A little later Giovanni Grassi demonstrated that indeed *Anopheles* could transmit malaria between people. Manson had believed that a mosquito bites only once, an influential error that proved something of a break on the concept of a vector. Recognition of Ross was unusually rapid, however, for he received the recently instituted Nobel Prize in 1902, and Laveran was thus recognized in 1907. Meanwhile, Manson initiated the London School of Hygiene and Tropical Medicine in 1899.

Human malarias involve only ourselves, mosquitoes and a few *Plasmodium* spp. They are anthroponoses. Such micro-organisms were called *sporozoans*, but are now included in the phylum Apicomplexa. *Plasmodium* and related genera have a long evolutionary history as parasites of tetrapods. Tropical lizards (Fialho and Schall, 1995) and birds (Lalubin *et al.*, 2014) suffer from malarias borne by mosquitoes and phlebotomid flies such as *Lutzomyia*. Several *Plasmodium* spp. are known from primates.

Four well-known species cause human malarias: *Plasmodium falciparum*, *P. vivax*, *P. malariae* and *P. ovale* (Escalante *et al.*, 1995), the clinical symptoms of which vary. They infect us as sporozoites from the mosquito's salivary glands. While >60,000 of them may exist in the mosquito's salivary glands, oddly very few are injected (Service, 2000). After infection there is an initial period of asexual reproduction in the liver followed by further asexual multiplication of merozoites in our erythrocytes. This stage causes the recurrent fever, characteristic of malaria, when a new crop is released into the blood. *Plasmodium vivax* and *P. ovale*, unlike the other species, maintain a long-term, dormant infection in the liver cells. *Plasmodium malariae* can also persist for decades in its host. This means it may survive in cool climates where vectors cannot fly during winter. During a final stage in human blood, male and female gamonts are produced which may be sucked up by another mosquito. This can occur even 2–3 weeks after the initial human infection. The plasmodia then reproduce sexually in the insect's midgut before moving to its salivary glands, potentially to continue the cycle as sporozoites in another human victim.

Development in mosquitoes normally takes ~10 days so that there is considerable, often >80% mortality of infected females during this period, so partially breaking the parasite's life cycle. For example, the daily survivorship in Senegal for *An. arabiensis* is estimated at 0.82 (Vercruysse, 1985) – only ~13% of a cohort would survive 10 days. Even so, up to 15% of *Anopheles* females carry infective sporozoites in highly endemic regions, although this figure is usually nearer 5%. This value, called the '*sporozoite rate*', is fairly typical for the related *An. gambiae* s.l., several being major African vectors. This is probably because they have relatively long-lived adults (Section **13.4.1**) that often live near people. While other culicines and anophelines may feed on flowers (Healy and Jepson, 1988), their life span is greatly increased by feeding on various *peridomestic* nectar sources, especially the foliar nectaries on cassava, possibly to >3 weeks (Gary and Foster, 2004). In contrast, *An. culicifacies* has a typical sporozoite rate of only ~0.1%. This mosquito has a short adult life and often bites cattle (van Emden and Service, 2004), so females full of cow's blood will not bite us (Section **13.2.4.4**). It is a major malarial vector in India (despite governmental claims that malaria has been eradicated!). But *An. culicifacies* populations may be so dense that one can get many bites. Similar relationships occur in the transmission of mucocutaneous leishmaniasis by sand flies (Section **7.3.2.4(b)**) and of sleeping sickness by tsetse (Section **7.3.2.4(n)**).

Temperature has various effects on the rate of *Plasmodium* transmission. At higher temperatures the parasite has a shorter life cycle in the mosquito, which thus becomes infective more rapidly. But mosquitoes, like most other insects (Section **10.2.3.3**), usually have reduced life spans at higher favourable temperatures. But the outcome on the transmission rate depends on several factors: the balance of temperature, the species of *Plasmodium*, and the species, nutritive state and biting rate of the *Anopheles*. In parts of West Africa, the transmission rate is so high that one can expect >100 *infectious* bites per year (the EIR = entomological inoculation rate) (Collins and Paskewitz, 1995). Rarely, EIRs >1000 have been recorded during the rainy season (Robert *et al.*, 2003). In such a situation even a large reduction in the population of vectors has little effect on the prevalence of malaria (Dye, 1992). It is worth noting in this context that West Africa was, and to an extent still is, a high-risk area for diverse diseases. In old colonial days it was called the White Man's Grave:

> Beware and betide the Bight of Benin,
> For few come out though many go in.

Plasmodium falciparum causes half of all human malaria. It is virulent and tropicopolitan, potentially affecting 25–60% of host erythrocytes, although not at once, and 15% so infected would be life threatening. It can also lead to complications, especially cerebral malaria, which can be rapidly fatal, to anaemia, to renal failure and to abortion. The great evolutionary thinker W.D. Hamilton died of such effects arising from his contracting malaria. When *Plasmodium* stimulates some of the white blood cells to multiply, it may increase the spread of HIV, making the doleful progress to AIDS itself more rapid (Section **7.3.2.4**(**b**)).

Plasmodium vivax is more widely distributed, being tropicopolitan and also found in Mediterranean and warm-temperate climes. It accounts for a further 44% of malarial cases, but in a milder form since, unlike *P. falciparum*, it is confined to young erythrocytes. These comprise only ~2% of the total. There is no cerebral involvement. A few years ago another similar species, barbarously called *P. vivax*-like, was separated from it. Conversely, *P. malariae* attacks old erythrocytes and accounts for the remaining 6% of cases, while *P. ovale,* apart from along the West African coast, is regionally rare. Recently, *P. knowlesi* has been detected in Borneo (Singh *et al*., 2004). Microscopically indistinguishable from *P. malariae,* this species was separated by a nested PCR assay identifying its DNA sequence. Of a sample of 208 malarial cases, 58% were *P. knowlesi*, which is thus new to people, although recorded previously from macaques, *Macaca fascicularis*. This *Plasmodium* has possibly been transmitted to us by *Anopheles leucophyrus*. Remembering, therefore, that *P. malariae* is found in chimpanzees, in which it is often called *P. rodhaini*, there is a limited zoonosis.

Work on *Plasmodium* genetics (Escalante *et al*., 1995) shows that while the species attacking us are widely separated from each other, with an evolutionary divergence of >100 million years, they show more recent genetic affinity to simian plasmodia. *Plasmodium vivax* is close to *P. simium*, while *P. malariae* is close to *P. brasilianum*, both species being found in New World monkeys. Again, *P. vivax*-like is close to *P. simiovale* from Old World macaques, while *P. ovale* has a simian counterpart in *P. schwetzi* (Ewald, 1983). Finally, *P. falciparum* is much like *P. reichenowi*, another parasite of chimpanzees, our closest relative. The origin and antiquity of *P. falciparum*, however, are under debate (Pennisi, 2001). Has it had a long history of infecting pre-human species or did it arise by mutation at the inception of agriculture some 10,000 years ago?

Worldwide, plasmodia are spread by ~70 species and sub-species of *Anopheles* (Service, 2000). No other genus is involved (Escalante *et al*., 1995). But the picture is more complex than can be given here, although we are dealing with it in relative detail. As improvements in taxonomy proceed, particularly by the development of chromosomal and molecular techniques, more and more old anopheline species are found to be species complexes (Section **1.3.4**), the adults being inseparable by microscopical means. It appears that some members of a species complex transmit malaria while others do not. This obviously confounds earlier fieldwork and emphasizes a *key role of searching taxonomic studies* (Walter, 2003) at the genomic level.

Each of the 20 or so *important* vectors mentioned here has its unique ecology as well as a definitive regional distribution, reasons why malariologists say: ‘every malarial problem is a local problem’. This saying, indeed, often applies to other pest situations. Some *Anopheles* select specific, localized habitats while others are more wide ranging (see Section **12.3.4.4**(**e**)). For example, *An. anthropophagus, An. funestus* (an important vector)*, An. minimus* s.s and *An. sergentii* select shaded breeding sites, but *An. albitarsis, An. arabiensis, An. gambiae* s.s., *An. labranchiae, An. quadrimaculatus* and *An. sacharovi* select sunny ones, while. *An. aquasalis* and *An. farauti* are found in both situations. Forest clearance and crop irrigation tend to increase our exposure to these vectors (Pennisi, 2001), while programmes to control them must be always suited to local conditions.

The main Palaearctic/Mediterranean *Anopheles* vectors are *An. sacharovi* and *An. labranchiae,* which are part of the *maculipennis* complex, which also includes *An. atroparvus*, *An. beklemishevi*, *An. martinius*, *An. melanoon* and *An. messeae*. Then there is *An. persiensis*, which has been separated recently, principally on DNA evidence, and is confined to the region north of the Caspian (for detailed analysis, see Sedaghat *et al*., 2003; Harbach, 2004). *Anopheles superpictus*, *An. sargentii* and *An. pharoensis,* a large beast found commonly in the Nile Delta, also belong to this major region. The original *Anopheles* studied by Ross in India was *An. culicifacies*, which has a very wide distribution across southern Asia. It often oviposits in recently planted rice paddies. This beast, together with *An. dirus*, *An. minimus* and *An. stephensi* and others, commonly transmit malarias in the Indian sub-continent and in South-East Asia, the latter species being important in urban areas. *Anopheles dirus* complex contains >7 species, with *An. dirus*

A and D being on either side of the Dawna Range on the Thai/Burma border, where they may hybridize (Walton *et al*., 2001). Recently, *An. culicifacies* and *An. minimus* themselves have each been shown to be complexes of four and two sibling species, respectively. Indeed, the Malayan region is very rich in vectors, with more than a dozen species. In Indonesia, *An. barbirostris* s.l. is an important vector containing four sibling species, while the *An. punctulatus* complex transmits *Plasmodium* in New Guinea.

In China, *An. anthropophagus* and *An. sinensis* are the main vectors.

The more arid regions of sub-Saharan Africa contain *An. arabiensis,* which is part of the *An. gambiae* complex (Coetzee, 1989; Hunt *et al*., 1998; Coluzzi *et al*., 2002; Fanello *et al*., 2002; White *et al*., 2011), and the wetter regions have *An. gambiae* s.s. and also *An. funestus* and *An. moucheti* as vectors. Several *Anopheles* breed in shallow ponds where cattle drink. The hoof prints fill with water, providing ideal breeding sites (patches) for mosquitoes as predaceous fishes are excluded. *Anopheles gambiae* s.s. itself is highly polymorphic, and like some *Drosophila* species, exhibits a variety of chromosomal inversions. It has S and M forms, which are based on fixed differences at the rDNA locus (Favia *et al*., 2001). These interbreed rarely (Tripet *et al*., 2005). Then, not all of these *strains* transmit malaria. For example, the L3-5 strain kills and then melanizes a variety of parasite species (Collins *et al*., 1986, in Blandin *et al*., 2009). The S-form, which is ancestral, breeds in rain puddles while the latter has evolved to inhabit irrigated sites and rice paddies. While *An. quadriannulatus* and *An. bwanbae* are in the *An. gambiae* complex, they are unimportant vectors as they rarely bite people, *An. bwanbae* being confined largely to thermal springs in Ugandan forests. This complex includes *An. melas* and *An. merus*, which are brackish water species from West and East Africa, respectively (White *et al*., 2011). Then in southern Africa, the non-vector *An. longipalpis* has long been confused with *An. funestus* (above). Misidentification leads to wastage of time and of funds much needed for malarial control.

Neotropical *Anopheles* include *An. albimanus*, *An. albitarsis, An. aquasalis*, *An. bellator, An. cruzii* and *An. darlingi*. In Jamaica, *An. albimanus* is common so that when infected persons are allowed to settle here the disease could again become rife. This species penetrates the southern USA, where *An. quadrimaculatus* and *An. freeborni* are potential vectors. The above provides students with an idea of the global complexity of the vectorial species. On the brighter side, if one worked on malaria in a limited region, say Brazil, there would be only a few species to deal with because as one can see from the above, *Anopheles* are *regional* in their distribution (see Table 2.1 in Service, 2000). Critically, longevity and the propensity to bite us make for a high intensity of transmission even at a low population density of the vector (White *et al*., 2011) and, of course, of the victim.

At the edge of endemic regions, such as parts of southern Africa and northern Argentina, the winter is cool enough for the adult vectors to cease activity and hence transmission stops, which also limits the cycling of *P. falciparum*. Conversely, during summer in temperate regions, infected tropical *Anopheles* occasionally escape from planes and transmit the so-called ‘airport malaria’ to unsuspecting local residents.

Anopheles gambiae s.s. transmits malaria with deadly efficiency, being highly anthropophagic and endophilic (Gary and Foster, 2004). It is the world’s major vector. It has found its way out of sub-Saharan Africa, where it is widely distributed, on several occasions – and may do so again. It reached Mauritius in about 1860, ultimately causing some 32,000 deaths from malaria. It took a plane to Brazil in 1930, and was the root of an epidemic that was not eradicated until 1949 after a massive effort. It got into Egypt in 1942, probably down the Nile by boat, but was eradicated in 1948 after WWII (Collins and Paskewitz, 1995). Rarely, where screening in blood banks fails, plasmodia, like HIV, can be transmitted from person-to-person in transfusions. The multiple use of a hypodermic needle among heroin addicts has a similar consequence.

In regions where malarial incidence is high, and was probably higher in the past, such as sub-Saharan Africa, the Mediterranean and parts of India, the human population possesses genetically determined blood polymorphisms that partially protect it. Most widespread is the Hb^a Hb^s system. These are alleles at a specific locus. People of genotype Hb^a Hb^a are unprotected, those of Hb^a Hb^s are protected, while those of Hb^s Hb^s suffer from the debilitating genetic disease *sickle cell anaemia*. In regions in which malaria is rife the gene frequency of the normal gene Hb^a is still greater (~0.8) in the population than that of the sickle cell gene Hb^s (~0.2), but this genetic system protects about 30%

of persons from malaria, while only a few per cent suffer the anaemia. The gene has been naturally selected for since progenies expressing it in the heterozygote have high survival, a situation called *over-dominance* or more explicitly *heterozygote advantage*. Apart from this blood polymorphism, people of West African origin often have another in which the Duffy negative phenotype is resistant to vivax malaria because it acts to produce a vasodilator. In East Africa, some persons have a gene giving a greater production of nitric oxide (NO), so reducing the effects of falciparum malaria (Hobbs, 2002). Nitric oxide is also present in the vasodilator produced by *Rhodnius* (Section **7.3.1.1**), and interferes with coagulation of mammalian blood. In the Punjab, persons carrying *P. vivax* are often asymptomatic (Herrel and Amerasinghe, 2004). In Rondonia, west Brazil, much of the indigenous population is asymptomatic to both *P. vivax* and *P. falciparum* infections (Alves *et al.*, 2005). Apart from these cases, adults surviving repeated bouts of falciparum malaria acquire partial immunity to it.

According to species, female *Anopheles* bite people either indoors (*endophagic*) or outdoors (*exophagic*). Endophilic mosquitoes can be controlled and excluded by screening windows and doors or by using bed nets treated with long-lasting insecticides like carbosulphan and deltamethrin (Permanet™). The repellence of pyrethroid-treated nets generally reduces biting of unprotected people, often children, in the same room. These nets can be washed regularly and re-treated, a solution that would have pleased Ronald Ross, and indeed pleases many local people today. If people have to pay a small price to buy a net they are more likely to use it! Exophilic mosquitoes are naturally more difficult to combat. Suitable repellents are DEET and DIPM (Section **7.2.3.4(c)**). Apart from fogging, sub-lethal doses of various insecticides may reduce the life span of mosquitoes and in train the sporozoite rate.

Traditional control of most anopheline mosquitoes, which commonly breed in sluggish streams and ponds, is best accomplished by manipulating larval environments. First, draining, for example in regions in which rice is grown in paddies, cyclic flooding and draining reduces the density of various mosquito species, including anophelines. Naturally, the duration of flooding must be shorter than the period of development and care must be taken to eliminate puddles. Meandering streams may be straightened and/or re-routed and marginal pools eliminated. Essentially, one aims to reduce the carrying capacity of the landscape (Sections **12.2.3.3** and **12.3.4.4**). Second, the water surface can be sprayed with a light oil to prevent the larvae respiring. Third, there are various options for biological control. The small, prolific fishes *Gambusia* and *Poecilia*, which are predators of the larvae and pupae, are commonly used, but it is uncertain how effective they are on a wide scale. It is certain they have caused the demise of some endemic fishes and damselflies (Howarth, 1991). In a trial with *Gambusia* in California *increased* mosquito numbers resulted. But in arid environments such as Afghanistan and Iran, where water is localized, they have had an impact. In other arid regions, the 'instant fishes' *Nothobranchius* and *Cynolebias*, which have drought-resistant eggs, may prove to be useful. In China, flooded paddies culture carp that deter mosquitoes, the fish being an added crop, and their faeces fertilize the rice (Section **13.2.4.6**). Work in New Orleans shows that *Toxorhynchites ambionensis* (Section **7.3.2.4(c)**) has a potential to control vectors such as *Ae. aegypti* that breed in containers (Pates and Curtis, 2005), and might be useful on *Anopheles* spp. with localized breeding, while *T. rutilus* has some effect on mosquitoes in tree holes. Species of *Culiseta* are sometimes opportunistic predators too (Blaustein and Margalit, 1994).

The bacterial endospore toxins produced by *Bt* subsp. *israelensis* and *B. sphericus* are effective on several *Anopheles*. They are best regarded as pesticides of living origin, but lack residual activity. Fungal pathogens such as *Coleomyces, Lagenidium, Culicinomyces* and *Metarhizium anisopliae* have been studied but show little promise (Collins and Paskewitz, 1995). The final control mechanism is larvicides, including organophosphates (e.g. malathion, fenitrothion and temephos), carbamates (e.g. propoxur) and pyrethroids (e.g. permethrin and deltamethrin) (Section **13.2.3.2**). There has been renewed use of DDT. It is cheap, not very toxic to us, and has a rather short life in the tropics. Also, since the larvae are filter feeders, small poisonous particles can be effective. Paris green (copper acetoarsenite) was so used to eliminate *An. gambiae* from Brazil. It is old fashioned but should not be discounted as it targets the filter-feeding larvae specifically. Although a total of >US$5 billion is spent annually on insecticides, only ~10% is used in public health schemes. Much of the resistance to these compounds mosquitoes have acquired is a backlash from their agricultural use, especially on cotton and rice. Consequently, several anopheline vectors, including *An. gambiae, An. arabiensis, An. culicifacies, An. minimus, An. stephensi, An. sacharovi* and *An. albimanus*, are resistant to many tradition organochlorines (Section **13.2.3.1**), some organophosphates and a few pyrethroids (Collins and Paskewitz, 1995).

The sterile male technique (SMT, q.v., Section **13.2.2.1**), which has been used so successfully against screw-worm in the New World (Section **7.4.1.2(d)**), is unsuitable for controlling mosquitoes as they have high natural mortality, breed so quickly and are surprisingly migratory (Johnson, 1969; Section **7.3.2.4(c)**). For example, an attempt to eradicate *An. albimanus* in 1976 from an area of a mere 20 km^2 in El Salvador, which involved *the daily release of a million sterile males for 4 months*, led to a considerable drop in its numbers. However, the immigration of fertile females prevented eradication (van Emden and Service, 2004).

There have been efforts to genetically engineer *Anopheles* spp. to render them incapable of malarial transmission (Ito *et al*., 2002; Alphey *et al*., 2002; Section **13.2.2.2**). Essentially, we try to help the mosquitoes resist *Plasmodium* and thereby stop transmission to us. For this technique we note that: (i) there are many species of *Anopheles*, a genus with incomplete taxonomy; and (ii) it is necessary to get the resistant varieties to spread in natural populations to the exclusion of the wild-type vectors (Burt, 2003). If the GM *Anopheles* become resistant to *Plasmodium*, they might also have enhanced reproductive success and hence oust the carriers.

Recall that not all *Anopheles* transmit malaria. Why is that? There will likely be physiological and ecological reasons. Parasites may have bad effects on their vectors (Dye, 1992). For avian malaria, fitness costs on *Culex pipiens* are centred on survival rather than on fecundity, and are severe in harsh environments (Lalubin *et al*., 2014). But in Tanzania *An. gambiae* carrying *P. falciparum* had a 17.5% loss of fecundity (Hogg and Hurd, 1997) compared to non-carriers. Then, some strains of *An. gambiae* trap *Plasmodium* ookinetes in a melanin capsule as they try to pass through its gut wall (Collins *et al*., 1986). These strains are totally resistant to the simian *P. cynomolgi* and partly resistant to *P. falciparum*, *P. vivax* and *P. ovale*. A genomic region, containing the *TEP1r* gene responsible for resistance to *Plasmodium*, exists on the left arm of chromosome 3 (Blandin *et al*., 2009). Other resistance genes (*APL1 A,B,C*) have been found on the left arm of chromosome 2 (Riehle *et al*., 2008, in White *et al*., 2011). Probably an ongoing evolutionary arms race exists between protist and potential vector. In addition, a class of antimicrobial peptides (AMPs) exists that kills early sporogonic stages of *P. falciparum* without harming the vector itself (Carter *et al*., 2013). The most effective ones are derived from aculeate venoms. We must now produce transgenic *Anopheles* expressing these AMPs. This whole field requires close co-operation between geneticists, insect ecologists and evolutionary biologists. Whether or not these plasmodia can evolve strains that can avoid encapsulation or poisoning remains to be seen. But a direct genetic approach is to try to eliminate the anopheline vector itself (Burt, 2003).

Quinine, extracted from the bark of *Cinchona pubescens*, was the first malarial prophylactic. It is extremely bitter. Schweppes wisely mixed it into their Indian tonic water in which, preferably with a small admixture of gin, it served for decades as a pleasant deterrent to *Plasmodium* parasites, particularly in the Indian sub-continent. Later the less palatable but more effective drugs paludrine and mepacrine were developed, although the consumption of 'G&T' was unaffected. Chloroquine and lately mefloquine have been generally efficient malarial prophylactics, while doxycycline also has antibacterial action. Primaquine clears the resting stages of *P. vivax* and *P. ovale* from the liver. But resistance by *P. falciparum* to these drugs is taking place because of course biological systems evolve, and chloroquine has unwanted side effects. Artemisins, from the Chinese plant *Artemesia annua*, are now used against resistant strains. Of course, the development of an effective vaccine, particularly against *P. falciparum*, is the ultimate solution, as it has been against yellow fever (Section **7.3.2.4(e)**). But 40 years of research has failed to produce one. However, in 2011 Rayner at Cambridge characterized the erythrocyte surface protein *basigin*, which *Plasmodium* merozoites use to identify and subsequently invade these cells. But in *P. falciparum* there are >50 proteins that somehow may be involved in the invasion process (Wright and Rayner, 2014), so the interaction is doubtless highly complex. Even so, human sufferers having survived several bouts of falciparum malaria are partially immune to further attack.

7.3.2.4(e) DIPTERA; NEMATOCERA; CULICIDAE; Culicinae. *Aedes aegypti*, *Ae. luteocephalus*, *Ae. africanus*, other *Aedes* spp., *Haemagogus* spp, *Sabethes chloropterus*. Yellow fever and dengue mosquitoes. The viral infection causing yellow fever (YF) is another important disease mosquitoes transmit. It is confined now to tropical regions of Africa (>90% of cases) and America (Wills, 1996; Barrett and Higgs, 2007). Formerly, however, cases occurred as far north as Quebec and as far south as Uruguay (Vainio and Cutts, 1998), but were especially severe in the lower Mississippi, USA. Strangely, it is not found in tropical Asia. Such viruses are often known as 'arboviruses', which might lead anyone with scant knowledge of the classics, upon which most biological terminology is based, to believe they are something to do with trees. The 'arbo' bit, however, is an acronym for '**ar**thropod **bo**rne'. Yellow Fever Virus (YFV) is a flavivirus (a name derived from 'yellow') having several strains and is transmitted by mosquitoes, but mainly by *Aedes aegypti*. This beast is a daytime biter with presently a pan-tropical and subtropical distribution, having arrived in the New World on slave ships. Presently, some 2.5 billion persons may enjoy the attentions of *Ae. aegypti* on a daily basis. As in many biting flies, she uses pulses of elevated CO_2 and subsequently human sweat as a cue to the proximity of her favourite food (Dekker *et al.*, 2005). Females often bite several times before being replete, a temperature-dependent behaviour that increases the transmission rate of any pathogen she may be carrying (Halstead, 2008). Another factor, however, is the concentration of viral particles in the human blood (*viremial titre*): when this is low the mosquito in her little meal may not pick up enough to transmit the pathogen. The virions multiply in the midgut epithelium, although different strains of the mosquito from different regions have different susceptibilities.

Although in 1881 C.J. Finlay suggested an association between the distribution of *Aedes* (then *Culex*) and the incidence of this disease, the work did not appear in a widely available journal until 1886. American army doctors in Cuba showed its transmission by *Ae. aegypti* in 1899, knowledge that helped the completion of the Panama Canal in the early twentieth century. In Havana and later in Panama, Major W.C. Gorgas instituted effective eradication programmes. It was also discovered that YFV was present in primates other than man, another zoonosis. Long-lasting vaccines and eradication have been very effective, so by 2018 although 600 million were at risk there are only some 200,000 cases per year and 30,000–60,000 deaths annually, with >90% in Africa. Compared to malaria a mere trifle.

Christophers (1960), originally a junior partner to Ross in India, made a life-long study of *Ae. aegypti*. He also distinguished himself by being, at 104, the oldest entomologist of note that ever lived (Fig. 7.8). The mosquito is essentially peridomestic, but there are genetically different forms that are endophilic and exophilic. They breed in water in flower vases, trays under plant pots, and in diverse rubbish thrown negligently into the garden (Fig. 7.9; Section **7.3.2.4(c)**). The eggs are laid just above the water level and may remain viable for at least a year. They hatch when wetted, but may require a few wettings to do so. In continuous breeding, hatching is suppressed by reduced dissolved oxygen associated with the presence of numerous large larvae. Temperature and day length may also be involved (Sections **10.2.2.2** and **10.2.3**). But the life cycle is typically short so that huge populations often build up after rain, as happened in Puerto Rico, although Sheppard *et al.* (1969) and others found no such effect in Bangkok. In this riverside city, water is always abundant in water storage pots and so the population may be regularly suppressed by its enemies. But competition for food (*scramble competition*) reduces the larval growth rate and some strains produce growth retardants (Dye, 1984; *interference competition*, Section **9.8**). The major effect, however, results from physical contact between large and small larvae at high density. In addition, adult survival is greater under warm, humid conditions (Halstead, 2008). Larval competition can reduce the resistance of *Aedes* mosquitoes to dengue virus, enhancing their ability to spread the disease (Alto *et al.*, 2008).

The various YF epidemics depend on continent and habitat. In Africa, there is the forest or 'sylvan' type in which monkeys are the main hosts. Although the zoophilic sub-species of *Ae. aegypti* (*formosus*) is present, it has little contact with people, *Ae. africanus* spreading the virus between monkeys. When these impudent beasts come to steal agricultural produce at the forest edge or in savannah other *Aedes* spp. (*Ae. furcifer*, *Ae. taylori*, *Ae. metallicus*) may bite them and then infect workers. Another point, probably relating to the rather recent introduction of YF to the Americas (cf. Diamond, 1999),

Fig. 7.8. Sir Rickard Christophers who, over many years, promoted the study of *Aedes* mosquitoes. Source: Wikimedia Commons.

is that it kills monkeys there but not in Africa. Farmers bring YFV to towns, where *Ae. aegypti* breeds in various forms of urban waste, and another cycle begins. The Neotropics are similar, but the forest cycle is mediated by *Haemagogus janthinomys* and *H. leucocelaenus*, and occasionally by *Sabethes chloropterus*. These mosquitoes bite foresters, who then bring YFV to towns, where *Ae. aegypti* is again the vector (Service, 2000; Barrett and Higgs, 2007).

The wide geographical distribution of *Ae. aegypti* may mean that its migratory powers are greater than generally thought; perhaps like frit flies it is a high flier. Note that Glick (1939; Section **10.2.4.5**) caught several mosquito species high in the air and most insects move much further during dispersal than during oviposition (Johnson, 1969). The usual view, however, is that the adults seldom fly more than 100–200 m, although Liew and Curtis (2004) recorded flight within a 320 m radius in Singapore. Another fact is that the global trade in second-hand motor tyres moves the diapausing eggs. But its wide global distribution is of long standing, quite unlike the regional ones of *Anopheles*, in which individual adults of some species can move 20 km.

In domestic situations, *Ae. aegypti* can be limited by keeping the garden clean and by changing water in flower vases every few days. I recently discovered >200 larvae in a vase in a hotel foyer in Phnom Penh, Cambodia. Water storage pots are a continuing source of mosquitoes, which piped water does much to eliminate. Water containers like old open oil drums, discarded buckets and tubs, are a major source of trouble (Chadee, 2004). This is 'ignorance in action' again, careless people acting inadvertently as ecological engineers (Section **10.1.2**) improving the domestic environment for *Aedes* mosquitoes. Barrera *et al.* (2008) found in Puerto Rico that underground septic tanks were a major breeding site for *Ae. aegypti* and *Culex quinquefasciatus*. Although in Argentina the incidence of flies breeding in old tyres is less with greater urbanization (Rubio *et al.*, 2013), these frequent breeding sites should be collected centrally, a 10% redeemable levy would suffice, and recycled. Female death rates are expected to be ~20%/day (Sheppard *et al.*, 1969), such attrition reducing a cohort of 100 mosquitoes to ~20 in a week. More recent work estimates death rates nearer to 10%/day. Some regard fogging to kill adults as rather cosmetic, since most of the population is juvenile at any instant. But because mosquitoes can transmit the virus after only a 4.5–7.0 day refractory period, in contrast to a longer period in malaria, every effort must be made to eliminate them. Refractory periods also occur in vectors of plant pathogens (Bressan *et al.*, 2006). Sheppard *et al.* (1969) estimated that fogging would give <50% kill. There is also the general point in population dynamics that killing an adult is 'worth more' than killing a juvenile, since the latter usually has little chance of becoming adult anyway, a relationship covered in the term '*indispensable mortality*' (Section **11.4.3**).

Hamilton (1967), following Hickey and Craig (1966), notes that *Ae. aegypti* shows genetic conflict in which a driving Y-chromosome produces strongly male-biased natural populations, an effect also known in *Culex pipiens* (Sweeny and Barr, 1978; Burt and Trivers, 2006). This may be more widespread in other mosquitoes, especially culicines, and is being considered as a genetic means of control (Curtis, 1976; Ribeiro and Kidwell, 1994; Burt, 2003; Section **13.3.2.2**). Yakob *et al.* (2008)

Fig. 7.9. Human rubbish thoughtlessly discarded in Thailand, perfect for culturing thousands of *Aedes* mosquitoes. Traditional human waste material, unlike modern plastic, rotted away.

investigated a dominant lethal gene (*RIDL*) that acts at the inception of pupation in *Ae. aegypti*, and could possibly effect control.

7.3.2.4(f) DIPTERA; NEMATOCERA; Culicidae. Mosquitoes transmitting other viruses. When it comes to complexity, the diversity of the mosquitoes themselves (Section **7.3.2.4(c)**) and that of the viruses they transmit, is a lifetime's study. Well over a hundred mosquito species transmit a total of >40 viral types to us. These viruses are commonly named after the locality from which they were first described, but several of them have different strains. For example, Venezuelan Equine Encephalitis Virus (VEEV) has 11 sub-types, although only three, IAB, IC and IE, have caused major outbreaks (Weaver *et al*., 2004). Here, the alternative hosts are monkeys, rodents and domesticated and feral mammals. Less frequently, other tetrapods such as marsupials, bats, birds and even snakes are hosts and these 'amplify' the virus, that is, viral numbers build up in them. A rapid spread of arboviruses over great distances is probable when migratory birds are hosts, at least, if they do not become debilitated by such infections. In addition, viral spread is often related to urban poverty, where people live close together with little protection: density dependence again (Sections **10.2.3.7** and **10.2.3.9**).

At present, arboviruses have broad regional distributions. An important New World group is the Togaviridae, the main genus being *Alphavirus*. It causes equine encephalitis: western and eastern equine encephalitis (WEEV and EEEV) and VEEV, mentioned above. For example, WEEV is short for the virus, WEE is short for the disease it causes.

These viruses are particularly severe in horses, of course, but debilitate and sometimes kill people as well. VEEV is found especially in coastal regions of Venezuela, Colombia, Ecuador and Peru, and much of Central America where horses are still in general use. Major outbreaks occurred from 1942–1946 in Peru, from 1962–1964, 1968–1969, 1992–1995 in Venezuela, and in 1993 and 1996 in Mexico. While this virus has a variety of vectors, *Culex* (*Melanoconion*) section *Spissipes* spp., *Psorophora* spp. and *Ochlerotatus sollicitans* and *O. taeniorhychus* are particularly implicated (Weaver *et al.*, 2004). Vertical transmission between successive mosquito generations via the egg, larva and pupa is known in WEEV (Fulhorst *et al.*, 1994), Ross River Virus (below) and Sand Fly Fever Virus (Section **7.3.2.4(b)**). In such cases male flies, which of course do not bite, are sometimes found to contain the pathogen, the short cut to identifying vertical transmission. WEEV and EEEV together with St Louis Virus (SLEV) (*Flavivirus,* Flaviviridae) are found in both North and South America. *Culex* and *Culiseta* spp. often transmit them, but so do *Aedes*, *Anopheles*, *Haemagogus*, *Psorophora* and *Wyeomyia*. Another *Alphavirus* is chikungunya, which is transmitted in Thailand by *Ae. aegypti* (Halstead, 2008) and recently (2014) became epidemic in Jamaica. A wide variety of arboviruses exists along the Peruvian Amazon where *Culex pedroi* and *C. gnomatos* are important carriers (Turell *et al.*, 2005). Ilheus Virus (Flaviviridae) has been isolated from *Psorophora ferox*, a vicious daytime biter of materos. Turell *et al.* (2005) also isolated several bunyaviruses in the genus *Orthobunyavirus*, including Caraparu, Itaqqui, Murutucu and Mirim.

Of the Old World arboviruses, there is West Nile Fever Virus (WNFV). This is an important flavivirus originally described from North Africa, but has spread to southern Europe and western Asia, and in 1999 was found in the USA (Kramer *et al.*, 2008). It is transmitted mainly by *Culex* mosquitoes, and also affects birds and horses. Rift Valley fever (RVF) occurs in Egypt, Uganda, Zambia and South Africa. Kokobera, Murray Valley and Ross River fever are Australian diseases. The latter is the most serious mosquito-borne disease there, with ~5000 cases annually (Russell, 2002). Kangaroos and wallabies carry the virus, which is often spread by salt marsh species of *Aedes* and *Culex*. Salinization consequent on the extension of wheat growing in south-western Australia has led to increased populations of the halotolerant vector *Ae. camptorhynchus* (Carver *et al.*, 2009). Bahmah Forest Virus (BFV) was discovered in 1992. Nearly 5000 cases were reported in Queensland, Australia, between 1993 and 2003 (Quinn *et al.*, 2005). The freshwater mosquito *Culex annulirostris* and also *Ochlerotatus procax*, a flood water species, transmit BFV. Sindbis virus is found in South Africa, Egypt, Malaysia and the Philippines, but there was even an outbreak in northern Europe in the 1980s. Kairi virus occurs in Brazil, Colombia and Trinidad. Japanese encephalitis affects Japan, eastern and southern Asia, India and Sarawak. Japanese Encephalitis Virus (JEV) is the most important arbovirus in rice growing areas, and is often fatal. It also occurs in domesticated pigs, which act as amplifying hosts (Mogi, 1984) or diversionary mosquito food according to the circumstances.

While many such viruses are spread by only a few mosquito species, for example JEV by *Culex tritaeniorhychus* (Mogi, 1984) and Kairi by *Aedes caballus*, *Culex spissipes*, *Wyeomyia* spp., Sindbis is transmitted by a wide variety of genera. And apart from mosquitoes, ticks transmit RVF, VEEV and occasionally WNFV. WNFV periodically kills horses in the Camargue region of France, the erstwhile marshy delta of the Rhone. It is often spread by *Culex quinquefasciatus* in the southern USA and by *C. pipiens* in the north, although other species are involved. Some authors, for example Cui *et al.* (2007), regard these mosquitoes as part of the *C. pipiens* complex: *C. pipiens pipiens*, *C. p. quinquefasciatus*, *C.p. pallens* and *C.p. molestus*. *Culex p. palens* is dominant in northern China. In several large North American cities, *C. p. pipiens* adults overwinter in sewers. Similarly, *Ae. aegypti* juveniles persist in subterranean situations in Queensland (Kay *et al.*, 2002, in Chadee, 2004). Such behaviours allow much larger numbers to survive than would otherwise be the case and provide graphic examples of the adaptability of mosquitoes and their human association. The number of known arboviruses and their vectors is likely to increase materially as research proceeds.

A well-known human arboviral disease is dengue fever, caused by a flavivirus that has at least four types (DENV-1 to -4), many strains (Halstead, 2008), and is still evolving (Barrett and Higgs, 2007). It is spread by several species of *Aedes* including *Ae. aegypti* and *Ae. albopictus* in which viral replication may take place, and also a few *Culex* spp. in which it does not (Huang *et al.*, 1992). Over 2 billion people are at risk (Yakob *et al.*, 2008) and ~50 million cases of this painful, debilitating disease, aptly called 'break bone fever' in Jamaica, occur annually. While rarely fatal, clinically it may present as dengue haemorrhagic fever or dengue shock syndrome, which *are* fatal and account for much of the 500,000 annual death toll. No vaccines of general use have yet been developed. In both Cuba and Singapore recent social programmes of cleaning up the domestic and urban environment to reduce *Aedes* numbers have been used with success.

Another case, which is of evolutionary interest, is the mechanical transmission of the myxoma virus among rabbits by fleas and mosquitoes (Williamson, 1992). When introduced to Australia the virus caused >99% mortality of infected rabbits (Lewontin, 1970). But its virulence rapidly decreased. As expected, selection at the individual level produced resistant rabbits. But when the field myxoma virus was re-tested against standard laboratory rabbits it was found to have become less virulent. The virions form a deme (population) in individual rabbits and transmission is improved the longer rabbits live, since vectors do not bite dead ones. Lewontin (1965) gives this as a rare example of *group selection* (see also Slatkin, 1987; Sections **9.6** and **11.2.3**).

7.3.2.4(g) DIPTERA; NEMATOCERA; Culicidae, Culicinae. *Culex quinquefasciatus* (= *fatigans*, and recently = *C. pipiens quinquefasciatus*), and other mosquitoes, including *Anopheles* spp., *Mansonia* spp. and a few *Aedes* spp., transmitting *Wuchereria* and *Brugia*, the filarial nematodes causing elephantiasis. Apart from transmitting protistan and viral diseases, mosquitoes, and some simuliid and tabanid flies, also transmit pathogenic filarial worms. Their eggs develop into minute (~300 μm) microfilariae that live for long periods in human blood and lymphatic systems and also in those of higher vertebrates. In a typical life cycle, a mosquito ingests the microfilariae when she takes a blood meal. In *Wuchereria* and *Brugia* they further develop in her thoracic musculature and become infective larvae. These may be up to 2 mm in length when they have completed their development, a process taking ~10 days. They then invade the mosquito's mouthparts and should she take another blood meal, escape *onto* human skin. *Then* the infective larvae move through the feeding puncture into our lymphatic system, taking several months to develop. Now they are in the major lymphatic vessels and the lymph nodes. Female *W. bancrofti* measure *5–10 cm*, the males somewhat less. Should the sexes meet they mate, producing eggs and new microfilariae. The cycle is anthroponotic.

The presence of these huge worms in the lymphatic system, which may continue for several years, causes an inflammatory response leading to grossly swollen tissues. In severe cases one or both legs may swell to somewhat resemble an elephant's leg, hence the name *elephantiasis*. Clinically, thickening and dyspigmentation of the skin occurs as a result of chronic lymphoedema and fibrous infiltration. In the Eastern Caribbean the disease was known as 'Barbados leg' and associated with immigrant Indian indentured labourers. But swelling in other peripheral body regions such as the arms and scrotum, should the victim have one, may also occur. An estimated 1.1 billion persons are at risk from these worms and there were some 120 million cases of infection, 40 million of them severe and chronic, in 2001. The WHO is now promoting several campaigns using the drug diethylcarbamazine (DEC) to eliminate filariasis by 2020. The international pharmaceutical giant GlaxoSmithKline has freely donated the new drug albendazole, which is used in conjunction with ivermectin, donated by Merck, to treat the disease. Good things come from the multinationals too!

Culex quinquefasciatus is nocturnal and tropicopolitan. It has the distinction of being the first insect shown to be a disease vector. In 1877 Sir Patrick Manson found it transmitted *Wuchereria* in China (Section **7.3.2.4(d)**), who believed that mosquitoes returned the worms to water during oviposition, from which they re-infected man. But other unsung heroes had a part in this story. Alekji Fedchenko in 1870 described the life cycle of the Guinea worm, *Dracunculus medinensis*, and found an alternate host, a cyclopoid copepod. If crustaceans could be intermediate hosts, why not insects? Then the Australian parasitologist, Thomas Bancroft, suggested that the filariae were transmitted via the fly's mouthparts, which George Low showed in 1900 to be the case (Cox, 2002). Filariae are spread by ~60 species of *Anopheles*, *Aedes*, *Culex* and *Mansonia* in tropical and some sub-tropical regions. The vectorial species are different depending on the area and ecological situations (Section **7.3.2.4(c)**). For example, in many tropical regions *Anopheles* spp. can transmit not only malaria but also filariasis. *Culex quinquefasciatus* commonly breeds in polluted water especially pit latrines, from which it can be excluded by pouring small polystyrene beads into these nether regions, thus forming a physical barrier to ovipositing females. It also breeds massively in coir pits that are used to soak coconut husks prior to making matting. These should be located far from human dwellings, an imperative not easy to achieve in practice.

Brugia malayi and *B. timori* are transmitted similarly but confined to parts of South-East Asia, and while *W. bancrofti* tends to be urban, *Brugia* are more rural. Adult worms in people are ~3–10 cm long and produce microfilariae ~200–300 µm long. As in *W. bancrofti*, they circulate in the peripheral blood during the night and so may be ingested by nocturnal mosquitoes: *Culex*, *Anopheles* and *Mansonia* spp. A Pacific strain of *W. bancrofti,* however, circulates in this way during the day and day-biting *Aedes* transmit it (Service, 2000). These movements within our circulatory system are alternative dispersive strategies by the nematode.

7.3.2.4(h) DIPTERA; NEMATOCERA; Simuliidae.

Simulium spp. Black flies or buffalo gnats. These cosmopolitan, often numerous midges comprise over 1700 species in 26 genera, but only *Simulium*, *Prosimulium*, *Austrosimulium* and *Cnephia* bite people. They are poorly represented in the fossil record, being known only since the Oligocene. Females, sometimes in congregations (Coupland, 1991), oviposit at the water's edge, on aquatic vegetation or even under the water. Several species lay batches of 150–600 eggs, taking a blood meal in between ovipositions. Unlike most mosquitoes, females may live as long as 80 days. Thus, achieved fecundity may be >1000. As in mosquitoes, *Simulium* larvae are generally aquatic filter feeders on small organisms and organic particles. They trap these in a pair of large cephalic fans held in the water current. Even so, cannibalism among them is known. While larval mosquitoes are present in a variety of watery situations, simuliid larvae are found only in running water, usually in rivers and streams and often in concentrations near waterfalls and rapids, although constantly running drainage water from houses may suffice. They are effectively sessile, attaching themselves by a posterior circlet of hooks to various submerged substrata on which they spin a silken pad. On sunken boulders the larvae seek superficial areas where the flow of water is high, but pupate on the back face. The silk is produced from the salivary glands and they also spin lines in the manner of moth larvae. A limited locomotion is possible either by using these lines or by using the posterior hooks alternately with a hooked proleg on the thorax, and progressing in a looping motion. However, they are sometimes carried long distances downstream in spates, when it is likely that most of them perish, a case of severe episodic mortality caused by a physical factor (Section **10.2.3.6**). They are prey to plecopteran and odonate nymphs and diverse fishes. The pupae are immobile and contained in a loose cocoon. Since, unlike most mosquitoes, they have gills, neither larvae nor pupae need to breathe at the water surface.

The adults are compact little flies often ~3–4 mm long and quite unlike mosquitoes. The eyes are well developed and in the males the upper facets are enlarged. They have a humped thorax, the origin of the descriptive American name 'buffalo gnat'. The wings are short and broad, although longer than the abdomen, without scales and the venation posterior to the radial vein is weak. A feeding female anchors her proboscis to the skin with labral and hypopharyngeal hooks, and then slashes with her mandibles. A minute 'pool' of blood is formed that is sucked up (Section **7.3.2.3**). *Simulium* may also take nectar, usually from inconspicuous flowers.

7.3.2.4(i) DIPTERA; NEMATOCERA; Simuliidae.

Simulium damnosum s.l., other *Simulium* spp. Cosmopolitan flies transmitting filariae causing river blindness (sub-Saharan Africa, Neotropics) and bovine onchocerciasis. *Simulium damnosum* s.l. is widely distributed in tropical Africa, limited by the Sahara in the north but reaching Mozambique in the south. It transmits the filarial nematode *Onchocerca volvulus* as an anthroponosis. This worm infects people (*human onchocerciasis*) causing dermatitis and blindness, which, because of its association with flowing waters, is called *river blindness*. It will bite after flying more than 10 km. As in several *Anopheles*, this *Simulium* is a species complex (Dunbar, 1966, in Laird, 1981). There are some 40 chromosomal patterns and about 24 named sibling species, not all of which are vectors. Within this complex, considerable geographical and ecological separation occurs. In West Africa, *S. damnosum* s.str. and *S. sirbanum* are found more to the north in savannah, while *S. yahense* and *S. sanctipauli* favour forest streams in the south. Occasionally, wind-assisted migrations spanning >400 km are recorded, and these, as with migrant armyworms and locusts, are associated with the seasonal passage north of the Inter-Tropical

Convergence Zone (Pedgley *et al*., 1995; Section **2.2.2.1**). *Simulium neavei*, whose juveniles are phoretic on freshwater crabs and mayfly nymphs, also transmits *O. volvulus*. Its more limited distribution is centred in Congo and Uganda (Crosskey, 1990).

The nematode itself was probably transported in enslaved people to tropical South and Central America, where *Simulium guianense*, *S. ochraceum*, *S. metallicum, S. callidum* and *S. exiguum* became the new vectors. Human movement transports disease as surely as insect movement does. But despite the existence of a species complex in *S. damnosum* the vectors are few compared to those of several preceding diseases. Microfilariae are picked up from the skin, not the blood, of infected persons by female *Simulium*. Development, taking about a week, proceeds to the third larval stage in the flight muscle. Surviving females may then infect another person through a feeding puncture. Adult worms in dermal nodules start to produce microfilariae 6–12 months after infecting a human host, so becoming a reservoir of further infection. Although other dermal symptoms occur, damage to the eye, often resulting in blindness, is caused by an immunological reaction to the presence of the microfilariae, and/or of *Wolbachia* (Section **10.2.3.9**) their bacterial symbiont.

According to WHO data, about 120 million persons were at risk and 18 million infected in 2001, of which about 17 million were in Africa. Some 270,000 people living in 2016 had been blinded by the disease, while a further half a million suffer impaired vision. The distribution of the disease, however, relating to the larval ecology of the vectors, is very patchy. There are major concentrations in eastern Senegal, in southern Burkina Faso and adjacent areas of Ghana, Togo and Benin, in highland regions of Nigeria and Guinea, southern Congo and northern Angola, and the watershed of the Upper Nile in southern Sudan and as far south as Lake Nyasa. In the Americas the disease is described from Ecuador, Colombia, Venezuela, Guatemala and southern Mexico.

In endemic areas where the human population is concentrated along the banks of a fast-flowing stream and where the land is best for agriculture, over half the people may be infected and up to 20% are blind. Migrant *Simulium* generally fly along rivers or the edge of gallery forest, thus spreading the disease. A general survey of 600 West African villages in 1991 revealed a disease prevalence of 33%. When a community abandons a riverside village to avoid this disease, they must still go to the river to wash and collect domestic and irrigation water, and may thus become infected, although to a lesser degree. Piping water underground from an upstream source to still, well-covered reservoirs is a good solution, but one difficult to maintain.

Overall reductions to *Simulium* populations may be made by other types of water control, such as cleaning streams of vegetation and building a series of mini dams for hydro-electricity and irrigation. But below a dam the stream often becomes an improved habitat for the flies. It must therefore be treated with insecticides (carbamates, organophosphates such as temephos and even DDT), to kill the larvae. *Bti* toxin has also been used, particularly where resistance to traditional insecticides has developed. From Guinea to Benin the disease has been subject to a massive control programme by the WHO, which at a cost of over US$500 million has had great success in reducing the prevalence of the disease to only 2–3%. From 1988 the microfilaricide ivermectin (Mectizan) (Section **13.2.3.1**) has been given orally to people (once or twice a year) to eliminate the microfilariae.

In this case using DDT can be justified, despite its environmental drawbacks, on the basis of cost and efficacy when set against the human misery and lack of fulfilment resulting from the disease. Unlike leishmaniasis vectors, with their diffuse distribution in the Neotropics, control of *Simulium* is feasible because of the more restricted area of their distribution and their specific requirements for breeding. A slug of insecticide dumped in the headwaters of a river will wash down it, killing the larvae. Such is a weak link in the pest's ecology.

Worldwide, biting *Simulium* spp. are some of the most intolerable pests, travelling as far as 400 km from their breeding areas. Glick (1939) trapped *S. occidentale* up to 1800 m in the air. Severe attacks on people may lead to dermatitis. In North America *Simulium* spp. may attack cattle and horses in such numbers as to kill them: *S. acticum* has been recorded doing so some 100 km from its nearest breeding site. *Prosimulium mixtum* (= *hirtipes*) bites fishermen in May and June in hilly regions of north-eastern USA. In similar regions of Europe, *S. reptans* breeds in big rivers and bites livestock. With other *Simulium* spp. it spreads bovine onchocerciasis caused by *Onchocerca* spp. (Coupland, 1991). In Queensland, *Austrosimulium pestilens* bites people and livestock alike and also transmits bovine onchocerciasis. Here, cattle have suffocated on dense swarms. In the Himalayas the potu fly, *Simulium indicum*, is an aggressive biter. Plagues of *S. colombaschense* occur periodically along the Danube, causing distress to persons and domesticated animals. In an extensive outbreak in 1923, >17,000 cattle, horses and other livestock died as a result of their bites.

Simulium venustum transmits *Leucocytozoon anatis*, which affects ducks (Hill, 1997) and in the eastern USA, *S. jenningsi* spreads *L. smithi,* which afflicts turkeys. Some other species of this *Simulium*-borne protist affect birds such as rooks, owls and passerines. *Simulium jenningsi* is an insistent nuisance biter and breeds in large unpolluted streams. In contrast, a few Arctic *Simulium* do not bite, relying on larval resources for oogenesis.

7.3.2.4(j) DIPTERA; NEMATOCERA; Ceratopogonidae. *Culicoides*, *Leptoconops*, *Forcipomyia*. Biting midges. Cosmopolitan nuisance biters and occasional vectors of disease. These are minute but important nuisance biters of man. Over 5000 species, of which >1200 belong to *Culicoides*, have been described. Like mosquitoes, they possess CO_2-sensitive sensilla on the maxillary palps. Again, there are autogenous and anautogenous types. For example, *Culicoides furens* in Florida can produce up to 60% of its maximum potential without a blood meal (Linley *et al*., 1970). Several species suck the haemolymph of insects: *Forcipomyia* is recorded from dragonfly wings and other species from engorged mosquitoes, although the sub-genus *Lasiohelea* within it bites people. Their small size (1–2 mm in length) allows them to pass through mosquito netting in formation flight, as it were, and inflict numerous bites. In the Amazon Basin, one may expect to be bitten by them (locally *marrahuee*) at least 100 times per day, mainly at dawn and dusk. On Caribbean beaches as the sun sets *Leptoconops* comes to bite you, hopefully with a planters' punch in your hand to mitigate its negative effects. But, like phlebotomine flies, they also need nectar.

As in some other Nematocera, mating swarms of males form in relation to markers such as boulders, fence posts and overhanging branches. These swarms serve as a large, mobile object that nubile females can presumably locate more easily than a lone mate. Rapid mating rather than mate choice seems to be key for such short-lived insects (Section **9.1**). Larval environments are generally wet, either fresh or brackish, with a high content of rotting organic matter, upon which they feed. Some *Culicoides* (*C. milnei*, *C. grahamii*) even feed in cut and dying banana pseudostems. Life cycles tend to be relatively short – under a month in warm conditions.

For all their insistent biting these midges transmit few human diseases, although recently they have been shown to spread several species of the filarial nematode *Mansonella* (Mellor *et al*., 2000). *Culicoides grahami* and *C. milnei*, among other species, transmit the filarial worms *M. streptocerca* and *M. perstans* (formerly *Dipetalonema)* in parts of tropical Africa. In Haiti, Trinidad, St Vincent and several islands in the Eastern Caribbean, the salt marsh species *C. furens* transmits *Mansonella ozzardi*. Despite its diminutive size, it may travel at least 1 km from its breeding site. Several species of *Culicoides* and *Simulium* spread this nematode in parts of tropical South America. Infection is often asymptomatic but the worms sometimes cause skin lesions, mild fevers and headaches. It has been suggested, however, that chronic arthritis is associated with repeated infections. Anderson *et al*. (1961) isolated Oropouche virus (Bunyaviridae) from a charcoal maker in Trinidad. Later, after outbreaks of the dengue-like disease it causes along the Amazon and other parts of Brazil, *Culicoides paraensis* was identified as its major vector. This midge and *C. insinuatus* are the major vectors higher up the Amazon in Peru (Mercer and Castillo-Pizango, 2005).

In addition, *Culicoides imicola* carries the reovirus causing blue tongue disease of ruminants, which can be serious in sheep and some deer, although it can replicate in other ruminants. Formerly confined to Africa and the Middle East, it now affects southern Europe, possibly as a result of the climatic changes associated with global warming (Section **2.2.2.1**). While there is substantial evidence for such a northward movement in some groups, such as European butterflies (Parmesan *et al*., 1999), northward movement in *C. imicola* is at best equivocal (Section **12.3.4.1**). Other suspected vectors of this disease in Europe are *C. scoticus, C. obsoletus, C. dewulfi, C. chiopterus* and *C. pulicaris*. *Culicoides* spp. also transmit a virus causing African horse sickness.

7.3.2.4(k) DIPTERA; BRACHYCERA; Tabanidae (~4000 spp.). Horse flies. Rather large, daytime nuisance biters and occasional vectors of disease. This family has a global distribution and is commonly associated with low-lying woodlands and marshes. Of the >30 genera, three are common, painfully mordacious and transmit a variety of disease organisms (Foil, 1989). *Tabanus* and *Chrysops* are cosmopolitan but *Haematopota* is absent from South America and Australasia. A fourth, *Hybomitra*, occurs in western USA. In the Amazon Basin, *Lepiselaga crassipes*, a small black horse fly, is an abundant and troublesome biter. Tabanid flies appear to have developed as micropredators in relation to the evolutionary expansion of ungulate mammals in the late Tertiary. Large batches of waterproofed eggs are laid on vegetation near the larval environment. Such egg clustering is odd when the adult females are highly mobile (Section **10.2.5.2**); the latter functioning to chase prey. The larvae live in shallow waters or moist soils, but seek drier places to pupate. *Tabanus* and *Haematopota* larvae eat small invertebrates and have a taste for cannibalism, while those of *Chrysops* are detritivores. Carnivorous tabanid larvae often bite the feet of workers in rice paddies. In most regions the life cycle is normally annual but may extend to 3 years under unfavourable conditions. While both sexes feed on nectar and pollen (Allan *et al*., 1987), only the females bite terrestrial mammals. *Tabanus* is essentially a biter of horses and cattle. Like tsetse (Section **7.3.2.4(m)**) they prefer to bite dark mammalian skins or clothing (Service, 2000), so that white is the garb of preference! The lack of any sneaky approach in *Tabanus* (Fig. 7.10) warns anybody as to their intentions. In the New Forest in Hampshire I once netted several big female *T. sudeticus* as they noisily circled me with malice aforethought. But cattle and wild ponies are frequently bitten, and the wounds may become foci of further infection, often by flies causing wound myiasis (Section **7.4.1.2**). As in mosquitoes and tsetse, CO_2 is a cue to the presence of prey, but their eyes are very large and vision is important. In pursuit they appear efficient: large *Tabanus* have maximum speed when chasing of ten times their cruising speed. The stress caused when pursuing cattle leads to a loss of production.

Chrysops, which often attacks the back of your neck, and *Haematopota* (the blood drinker), which sneaks onto the lower part of your leg, gain greater success as people biters than *Tabanus*. *Chrysops fuliginosus* and *C. atlanticus* are nuisance biters on the eastern seaboard of North America. In marshy regions of Russia, biting by *H. pluvialis* may be so severe as to make agriculture very unpleasant, particularly as the rewards in the past have not been commensurate with the efforts expended. Spraying oil onto the ponds in which they breed gives a measure of control, but when the breeding sites are diffuse it is inefficient and unfriendly to the environment.

Fig. 7.10. *Tabanus lineola*, a large horse fly showing the huge colourful eyes, short antennae and stabbing mouthparts. Source: Wikimedia Commons, photographer Thomas Shahan.

7.3.2.4(l) TABANID FLIES AS VECTORS OF DISEASE. *Chrysops* transmits *Francisella* (= *Pasturella*) *tularensis,* the Gram-negative bacterium causing tularaemia in large domesticated ruminants, but people also catch it. There are reservoir populations of *F. tularensis* in wild deer and in some rodents. The African *Chrysops dimidiatus*, *C. silaceus*, *C. centurionis* and *C. langi* transmit *Loa loa*, another filarial worm affecting the human eye (Section **7.3.2.4(i)**), although it does not cause blindness. These vectors are found in rain forests in a region roughly similar to that for Gambian fever (Section **7.2.3.4(n)**). The first two are day biters attracted to human activity; the second two are nocturnal or crepuscular and normally bite sleeping monkeys. But the main effect of loiasis is to cause periodic swellings or 'fascia' under the skin and over muscle, known as Calabar swellings. In 1995 there were some 33 million human cases. In northern Africa and parts of Asia, *Tabanus striatus* mechanically transmits *Trypanosoma evansi*, which causes Surra of horses, cattle and dogs. In camels the disease is known as el-debab and is frequently fatal. Tabanid flies also transmit *Tr. theileri,* which affects cattle worldwide. In Central and South America tabanid flies transmit *Tr. vivax* to cattle and sheep. *Tabanus* species may also spread anthrax caused by *Bacillus anthracis*.

7.3.2.4(m) DIPTERA; CYCLORRHAPHA; Muscidae; Glossinae. *Glossina* spp. Tsetse. African vectors of human sleeping sickness and nagana of cattle, pigs and horses. Dogs are also susceptible. 'Tsetse' refers to 'the fly that destroys cattle' possibly having origin in the Setswana language from Botswana (Gomani, personal communication) and has become incorporated in Swahili and thereby English. So one should call them 'tsetse' and not 'tsetse flies', as is often done: we do not call 'mosquitoes', 'mosquito flies'. Many native African languages where tsetse exist have their own word for these worrisome beasts. In the Rukiga language of Uganda the word is 'ebijuju', in Kikuyu it is 'mitzie' (Vaporidis, personal communication), in the Volta region of Ghana it is 'momoto', names revealing the longstanding importance of tsetse in parts of Africa. However, tsetse that bite people are absent from deeply forested regions, so in southern Nigeria there is no Igbo word for them, although *T. tachinoides* bites pigs there (Service, 2000). A study of such names would provide historical data on tsetse distribution; however, there are few dictionaries in African tribal languages, even though there is a pressing need for them.

Because tsetse have piercing mouthparts, close their wings scissor-like when at rest and have larviparous reproduction these peculiar muscids are often placed in a separate family, the Glossinidae, one showing some similar biofacies to the viviparous Pupipara (Section **7.2.2.1**). Both males and females bite and possess an obligate symbiotic bacterium, *Wigglesworthia glossinidia*, in special receptacles in the anterior midgut, providing essential nutrients (Baumann, 2005; Dale and Moran, 2006). They often harbour *Wolbachia* (Section **7.3.2.4(i)**), although its effects are uncertain, and a facultative symbiont *Sodalis glossinidius*. While now confined to Africa, fossils from the Oligocene shales of Florissant, Colorado, USA, show that tsetse once had a far wider distribution. But with global warming, should it continue (Section **2.2.2.1**), their distribution within Africa may further contract as they are sensitive to desiccation. Indeed, when the viral disease of rinderpest, introduced in Indian bullocks used to pull Kitchener's guns in the Boer War, decimated African ungulates at the end of the nineteenth century, they were at low levels, a situation that encouraged the importation of European cattle.

There are ~20 species of *Glossina*, but also several sub-species. They vary from house fly size to that of a blue bottle and are divided into three groups, which are taxonomically, as well as to a great extent ecologically, distinct (Table 7.2). The *fusca* group comprises large, forest flies that rarely bite people and do not transmit sleeping sickness. The dangerous ones are in the *palpalis* group (*G. palpalis*, *G. fuscipes*, *G. tachinoides*) found along rivers, lake shores, wet forest and luxuriant scrub, and in the *morsitans* group (*G. morsitans*, *G. pallidipes*, *G. swynnertoni*) found in dry savannah woodlands and thickets. This group also contains the rather odd, forest-dwelling *G. austeni* (Smith, A., 1973). Their distribution, as in *Simulium*, is determined by landscape, vegetation and microclimate, and is essentially patchy (van Emden and Service, 2004). Within 'fly belts' human habitation is effectively impossible.

Males are potent at 4–6 days old and females mate only once. Both require a few blood meals to complete development of their flight muscles (Marden, 2000). They may form aggregations, especially where game paths cross, and loose mating swarms at such times. As noted, adult tsetse desiccate easily, spending much of their time resting on trees and only a restricted period (<30 min/day) in

Table 7.2. Geographical distribution and habitat preferences in Africa of *Glossina* spp. transmitting trypanosomiasis. They are confined between 15°N and 20°S.

Habitat	West	Central	East
Forest and riverine habitats	*tachinoides* *palpalis*	*tachinoides* *fuscipes*	*tachinoides* (southern Ethiopia)
Savannahs	*morsitans*	*morsitans*	*morsitans* *pallidipes* *swynnertoni*

Data are from K.G.V. Smith (1973).

biting activity (Rogers and Randolph, 1985). They frequently pursue their prey, however, either man or beast, flying at up to 25 km/h. During these exertions they may open their spiracles to promote gaseous exchange, which leads to evaporative cooling, but only of 1.6°C or less (Edney and Barrass, 1962), and increased water loss. Indeed, desiccation, not hunger (loss of fat) is the main stimulus to feed (Jack, 1939, in Jackson, 1949). Later they return to forest or thicket to rehydrate, and perhaps digest their meal. Some species feed on avian and even reptilian blood.

As in the Pupipara, fertilized tsetse mature one larva at a time in a uterus developed from the common oviduct. A pair of nutritive glands serves the uterus and the larva consumes their secretions. The two ovaries ovulate alternately, a process delayed in virgins. Under field conditions the first offspring is produced when a female is 2–3 weeks old, and births continue at a rate of about one in 10 days, longer at lower temperatures. In *G. morsitans,* at 18°C this rate drops to one in 25 days, but genetic conflict may affect fertility in this species (Burt and Trivers, 2006). In *G. palpalis*, in particular, temperatures in the low 30°C permanently sterilize females. Optimal temperatures are 24–28°C, which affects female survival and pupal mass of the progeny and in train, fecundity. But she rarely produces more than ten larvae, often only five or less (Jackson, 1949; Service, 2000). Larval development is from 1–3 weeks, a duration largely influenced by the mother's ability to get blood meals. Three meals are usually required, but if food is short the larva may be aborted. Food availability depends on prevailing weather as well as the presence of mammalian prey. Females larviposit the mature progeny in damp, shaded pupation sites. Pupal duration is 4–5 weeks, even longer at lower temperatures. Humidity is critical for pupal survival, and flooding kills them. Older females may have survived for 3 months, older males rather less. Scars remaining in the ovary allow the number of offspring and approximate age of a mother to be estimated. Like *Stomoxys* (Section **7.3.2.4(o)**), tsetse accumulate florescent material in the head capsule, which may be used to age them (Lehane and Hargrove, 1988), although this process is also temperature dependent. The low potential rate of increase of tsetse contrasts with most higher Diptera (cf. *Musca*, *Cochliomyia* and *Lucilia*, below).

7.3.2.4(n) SLEEPING SICKNESS AND NAGANA. Sleeping sickness was formerly a major African malaise and still has an influence on human life there. Despite more than a century of attempts to control it (Jackson (1949) quotes nearly 100 papers, see Buxton (1955)), by the 1990s it was still a serious disease, affecting wide regions of Africa roughly between 15°N and 20°S of the Equator (WHO, 1998). The spatial scale of the control problem is thus comparable to that of the desert locust. In 2002 some 55 million people were at risk from sleeping sickness, with 300,000–500,000 cases and about 66,000 deaths annually. Some estimates are higher and in the 1990s there was evidence that its incidence was increasing. One should remember that when wars, civil or otherwise, break out (as in Rwanda) the control of diseases like this one is likely to go by the board, with the consequence of added human suffering. We need only recall the spread of typhus, trench fever (Section **7.2.1.2**) and malaria during WWI. But due to massive control efforts by trapping, the number of new cases in 2009 fell to less than 10,000, in 2013 to 6314, but increased to 9878 in 2015.

Together with a related variant in cattle, *nagana*, sleeping sickness is transmitted by several species of tsetse and caused by the protist *Trypanosoma brucei*. The related *T. congolense* causes only nagana. Recent DNA evidence shows that these African trypanosomes share a common ancestry of ~100 million years with *T. cruzi,* which causes Chagas' disease (Section **7.3.1.1**). There are three sub-species of *T. brucei* and six major species of *Glossina* in the *palpalis* and *morsitans* groups that transmit African trypanosomiasis. Firstly, *T. b. brucei* is a polymorphic blood parasite of antelopes and cattle, which are partly resistant and act as parasitic reservoirs (**13.1.2.2**). However, imported domesticated cattle, sheep, horses and pigs have scant defences against the disease. Both the above groups of tsetse transmit it. Secondly, *T. b. gambiense* causes chronic human sleeping sickness, also known as Gambian fever (Cox, 2002). It occurs in West and Central Africa from Senegal across to the south-west of Sudan, the whole of the Congo Basin and into northern Angola. It is probably confined to people and transmitted mainly by the *palpalis* group, although the western race of *G. morsitans* (below) is an occasional vector. These flies tend to appear where people gather to wash and collect water.

Within this vast region the distribution of the *palpalis* group is patchy as different species prefer different habitats. In the main they are thought to fly not more than a few hundred metres from their breeding sites, although they move more freely

(1–2 km/day) along rivers. *Glossina palpalis* is the most widely distributed species in West Africa with a sub-Saharan limit close to the 1150 mm isohyet and in the south following the coast from Senegal to the Namibian border. It is also found throughout the Congo Basin and prefers riverine vegetation and mangroves. *Glossina tachinoides* is more localized, being found further north in dryer regions well away from the coast and extending across to Sudan. Thus, it has a broadly similar geographical distribution to the western race of *G. morsitans,* but the former is a riverine species while the later inhabits savannah.

Finally, *T. b. rhodesiense* causes acute human trypanosomiasis (Rhodesian fever), in Central and East Africa in the area around Lakes Victoria, Tanganyika and Nyasa, but also in Zambia along the Zambezi Valley. A reservoir population exists in wild cattle. The disease is spread by the eastern race of *G. morsitans*. These are generally flies of the savannah and while there are subtle differences in their preferences, they often reproduce in gallery forests cloaking rivers. Using satellite imagery and associated techniques, Rogers and Williams (1994) predicted the distribution of *G. morsitans* in Kenya with 80% concordance with existing field data.

In such areas, hungry flies often cruise under the thin canopy of acacia trees fringing the gallery forest, particularly along a road or track. Bites away from shade are infrequent. Single bites rarely transmit the disease since most tsetse are ostensibly resistant to trypanosome infection and because the infected flies that bite people are often under the minimum age of 15–25 days to be competent to cause infection (Section **7.3.2.4(d)** and below). Disease transmission is rife because over a long period one can get a lot of bites.

The 'stumpy form' of the trypanosome is imbibed by feeding tsetse and multiplication occurs, at first in the gut and later in the salivary glands, so that as in malaria, a refractory period is necessary before a fly can become infective. Less than 0.1% of tsetse, however, are found by dissection to have infected salivary glands (cf. leishmaniasis, Section **7.3.2.4(b)** and the sporozoite rate in *Anopheles*). These trypanosomes multiply in the human lymphatic system, in our blood and later in other organs including the central nervous system. Drowsiness is the result of the encephalitis they cause. Gambian fever results from *low parasitaemia*. It progresses slowly if untreated. It starts with bouts of drowsiness, apathy and mental dullness, and continues for 1–2 years with headaches and body tremors followed by paralysis, convulsions and a further slow decline: emaciation, long periods of unconsciousness, coma and death. Rhodesian fever results from *high parasitaemia* that constitutes an acute challenge to the immune system, but lasts only 6 to 12 months. Towards the end of the nineteenth century this form of the disease killed some 250,000 people around Lake Victoria.

Nagana is typically rapid: if cattle are left to themselves they lay down and soon die. Losses to livestock recently have been estimated at £3 billion annually, affecting 37 countries in the region. Cattle that are tolerant of trypanosome infection include the N'dama longhorns and the West African shorthorns or Muturu. These breeds have arisen as a result of generations of natural selection by this disease and other environmental factors, but are not as productive as several susceptible or partly susceptible breeds. Cattle can be treated directly by applying pyrethroids (cypermethrin, deltamethrin), which reduce local densities of tsetse rapidly, but for sustainability ranches must be flanked by a barrier of traps (targets, see below) (Hargrove *et al*., 2003).

Because these flies desiccate easily, destroying gallery forest eradicates most of them, but of course this also degrades the environment. Clearing understory vegetation alone, however, is effective in reducing breeding habitats. This may be partly because the flies prefer to rest low down where the humidity is usually higher than above. Resting sites are up to 1.5 m above the ground in the dry season and up to 3.5 m in the wet season. Applying insecticides to the bush, which was done with great abandon with the advent of DDT, was not permanently successful. Subsequently, targeting the resting sites with organophosphates and more recently with synthetic pyrethroids has met with greater success, again relating to the sensitivity of tsetse to low humidity.

Tsetse are more attracted to solid colours than to striped ones. Perhaps the coat pattern of zebras improves their concealment from these flies (Waage, 1979). Work on indigenous hosts (Symes and McMahon, 1937, and Harrison, 1940, in Jackson, 1949) failed to implicate zebras. Pheromones acting at distance are unknown and so cannot be used to trap tsetse. Elevated CO_2 levels, however, which they can detect as far as 60 m from a mammal, act as a behavioural activator inducing attraction and landing (Guerenstein and Hildebrand, 2008).

The SMT (Section **13.2.2.1**), used so successfully with *Cochliomyia* (Section **7.4.1.2(d)**), would be appropriate here (Knipling, 1955), since females generally mate only once, are relatively long lived and have a very low fecundity. Although trials met with local success, for example, in Nigeria against *G. palpalis*, on the wide geographical scale of their African distribution such reductions have been temporary and insignificant. Flies soon move into the treated areas and restart disease transmission (Rogers and Randolph, 1985), again underlining the significance of insect migration. *Glossina pallidipes* can move 1 km/day (Vale *et al*., 1988), and Hargrove *et al*. (2003) document its mass migration from Mozambique into Zimbabwe. Migration can be deduced because populations recover at a rate far greater than that possible under their maximum intrinsic rate of increase. Trials have aimed firstly to reduce the tsetse population by using aerial sprays, followed by the release of hundreds of thousands of sterile males. Even so, the flies were not entirely eradicated. One of the problems is that females, showing vital discrimination, avoid sterile males as mates. Biocontrol with the eulophid wasp *Nesolynx albiclavus*, which seeks the puparia, has been disappointing too.

Catching the flies in conical traps impregnated with pyrethroid insecticide, however, has been much more successful locally and is a sustainable strategy because it requires only a small initial outlay of human expertise, equipment and finance. The efficient bi-conical trap comprises an upper inverted cone of white mosquito netting covering a lower cone of dark blue cloth with large holes for the flies to enter. The contrast in colour and also its background may be why these traps are so attractive. Baiting them with acetone and/or 1-octen-3-ol improves their efficiency: they may attract flies entering an area of 50 m radius. Large screens of blue cloth impregnated with insecticide have also been used. Because tsetse have so low a rate of population increase, worthwhile reductions in population can be made. In the Ivory Coast trapping reduced the population by 80% in a month and by 99% after 5 months (Laveissiere *et al*., 1980, in Rogers and Randolph, 1985). Vale *et al*. (1988) reported a reduction in a population of mainly *G. pallidipes* in Zimbabwe in 600 km^2 to 0.01% of its original density. Improvements in trapping cost, durability and efficiency continue to be made. Hargrove (2005) developed a stochastic model of tsetse eradication, indicating that daily mortality rates of >4% are desirable. Higher rates can be achieved, reducing the time to eradication and improving the logistics of the operation.

7.3.2.4(o) DIPTERA; CYCLORRHAPHA; Muscidae; Stomoxydinae. *Stomoxys*, *Haematobia* and *Lyperosia*. Biting stable flies and their relatives. These muscid flies breed in dung, although *Stomoxys*, unlike the others, avoids fresh cow dung and can develop in diverse Augean filth, rotting plant material, silage and uneaten food. *Lyperosia* females rest on cows and lay eggs in their dung while it is still tepid. In California, *S. calcitrans* numbers decline in warm (>30°C), dry weather (Mullens and Peterson, 2005). As in tsetse, they use airborne chemical cues (e.g. CO_2, acetone and 1-octen-3-ol) to find their prey, biting cattle, horses and occasionally farmers. *Stomoxys calcitrans* transmits the spirurid nematode *Habronema muscae* which causes summer sore in horses. The cycle starts when the maggots eat the minute nematode eggs in horse dung, but development to the infective third larval stage occurs in adult flies, these larvae escaping into the horse when the flies feed. They also spread *Trypanosoma equinum*, which affects horses in South America. All these flies may transmit viral and bacterial infections, the damage depending directly on their density on the cattle. Since counts >1000 per animal are common, this is often substantial. Milk yield may be halved and the growth rate of beef cattle much reduced.

Other muscid flies, mainly female, swarm around cattle and cause stress. They include *Hydrotaea irritans*, *H. albipuncta*, *H. meteorica*, *Haematobosca stimulans*, *Morellia simplex* and *Trichopticoides decolor*. *Musca crassirostris* is odd within this genus since it sucks blood. Some of the above transmit *Corynbacterium pyogenes*, a bacterium causing mastitis in cattle (Hill, 1997). Two pteromalid wasps, *Spalangia cameroni* and *Muscidifurax raptor*, parasitize puparia of *Stomoxys* and *Musca*, and probably those of related flies.

7.4 Myiasis

7.4.1 Obligate myiasis

Flies commonly causing obligate myiasis belong to two families in the calyptrate Cyclorrhapha, the Oestridae and the Calliphoridae. Taxonomically, they have been classified in various ways, but here we adopt the simple scheme used by Kettle (1995). Functionally, they have been classified by Zumpt

(1965) as causing: (i) dermal/sub-dermal; (ii) nasopharyngeal; and (iii) intestinal forms of myiasis. The first functional type, with its more superficial association with the host, may be caused by flies either with obligate or with facultative behaviour, while in the last two types the flies are always obligate. In addition, oestrid flies have invariably an obligate relationship with their victims. Again, taxonomy and behaviour tie up.

7.4.1.1(a) DIPTERA; CYCLORRHAPHA; OESTRIDAE; Gasterophilinae. *Gasterophilus nasalis, G. haemorrhoidalis, G. intestinalis* and *G. pecorum*. Horse bots. These cosmopolitan flies have larvae (bots) that are gastric parasites of horses. According to species the eggs are laid in various places. The first two species (above) attach them to hair on the muzzle and lower jaw, while the third cements its yellow eggs to the front legs. The large *G. pecorum* lays numerous (1300–2400) black eggs on grass or other herbage, where they persist for up to three months, an egg distribution recalling that in Group 1 tachinid flies (Section **8.2.2.5(h)**). Infection occurs if the horse licks its hair, so removing the eggs or the young larvae, or grazes herbage-bearing eggs. The eggs hatch rapidly and invade the tongue. They may be found there as small reddish larvae, a colour due to the presence of haemoglobin. On passing into the second instar they move via the oesophagus to the stomach. Here the larvae of *G. intestinalis* attach themselves by their mouth hooks, *G. nasalis* moves on and settles in the small intestine, while those of *G. haemorrhoidalis*, as their name suggests, favour the rectum. Although they feed mainly on the products of digestion in the horse's gut, *G. intestinalis* larvae also attack the gastric mucosa directly and those in the pyloric region may block the passage of food into the small intestine. They induce ulceration, stress and loss of condition. This is of great concern in racing thoroughbreds and show jumpers. Mature larvae leave the host via the mouth or with the faeces and pupate in the ground. Under temperate conditions there is an annual generation, but in the tropics breeding is continuous. In the south of England the wild ponies of the New Forest that are heavily infested with bots fail to thrive and, with an additional burden of intestinal helminths, have a reduced life span.

The old method of combing out the conspicuous eggs by grooming is effective, although grooms should be careful since the young larvae may penetrate human skin. Cures employ organophosphate systemics either in the form of a large pill, as an admixture in the food along with anti-helminthics, or as an external drench. All valuable horses are routinely treated every 6 weeks and confined to the stable for a day so that their faeces can be destroyed. Garlic is often included in their diet (K. Bradley, personal communication) as this helps to deter biting flies such as *Lyperosia* (Section **7.3.2.4(o)**). Wild or badly tended horses are often heavily infested, providing a reservoir of potential infection to valuable animals (Section **13.1.2.2**).

7.4.1.1(b) DIPTERA; CYCLORRHAPHA; Oestridae; Oestrinae. *Oestrus ovis*. Sheep nostril fly. Adults fly on warm, sunny days and like warble flies (Section **7.4.1.1(c)**) do not feed. They are larviparous. Females dart into the sheep's nostrils and larviposit therein. These larvae attack the lower nasal mucosa, while the second and third instars move into the upper passages. In some temperate regions, larvae deposited early in summer complete their development rapidly, forming a second generation in August, while the majority takes 10 months to mature; possibly another example of risk spreading in time (Section **9.7**), since larval development occurs under rather constant conditions. Mature larvae leave the nose, or are sneezed out, and pupate in the soil.

Fig. 7.11. The back of a cow severely infested with the warble fly *Hypoderma* (Oestridae). These flies have now been eliminated from much of Europe. From *The MSD Veterinary Manual*, online version. Scott Line, ed. Copyright 2019 by Merck & Co., Inc., Kenilworth, NJ. All rights reserved. Used with permission. Courtesy Dr Jack Lloyd. Available at: https://www.msdvetmanual.com/integumentary-system/cattle-grubs/hypoderma-spp.

The larvae of these flies cause great distress to sheep, goats and occasionally to shepherds. Like warble fly larvae, they feed on inflammatory products, but larvae dying in the nasal passages naturally liberate toxins. Mobile larvae may find their way into the nasal sinuses, damage facial nerves or even end up in the brain. Brain damage and malcoordinated movements often result, a condition called 'false gid' to distinguish it from 'true gid' due to the presence in the brain of coenuri of the tapeworm *Taenia multiceps*. The few records of this fly larvipositing in people come from the Mediterranean and the Middle East (Kuwait), but also from Barbados, where back-bellied sheep are raised. Two other locally abundant oestrine flies affecting the nasal cavities of large domesticated mammals are *Rhinoestrus purpureus*, found on horses from North Africa to Mongolia, and *Cephalopina titillator* from camels in the Sudan, doubtlessly exacerbating their famous bad temper. *Oestrus aureoargentatus* attacks a variety of antelopes, and *Gedoelstia* spp. penetrate the orbits of their eyes, but apparently they tolerate the intrusion. *Rhinoestrus giraffae* is specific to giraffes (Zumpt, 1965).

7.4.1.1(c) DIPTERA; CYCLORRHAPHA; Oestridae; Hypodermatinae. *Hypoderma bovis*, *H. lineatum*. Warble flies. Pests of cattle in the Northern Hemisphere. These flies are distributed throughout the region between 25°N and 60°N. In Europe they fly from late May until late July. Adults do not feed or bite at all and have a life span of only 3–5 days (Scholl, 1993). The life cycle is annual. They oviposit in sunny weather, avoid shade, and it therefore seems probable that their emergence is initiated by a spell of warm weather. The smaller *H. lineatum,* which emerges earlier than *H. bovis*, approaches cattle more stealthily, often laying eggs in strings. The latter species darts at the animal, depositing an egg each time, generally on the legs. Fecundity is 300–650 in either case.

The larvae hatch and bore into the skin through hair follicles, the places of entry often becoming sore in heavy infestations, and sometimes septic. *Hypoderma bovis* oviposits mainly on the hind legs, the larvae then following the path of the sciatic nerve into the spine, where the larvae rest between the dura mater and the periosteum. The first instars of *H. lineatum* pass the autumn and early winter in the leg, chest and abdominal tissue, but then move to winter resting sites in the connective tissue of the oesophagus. Remaining in the first instar, both species move again in late winter to the subcutaneous tissue along the back, where they initiate warbles and become second instars. They cut a breathing hole with their mouth hooks and induce the development of the warble which is effectively a sac of connective tissue. Their presence causes suppuration, upon which they feed, while producing bacteriostatic compounds to prevent bacterial colonization. The duration of the second and third instars are 15–50 and 25–35 days, respectively. When mature, the larva squeezes itself out of the warble, leaving a conspicuous hole (**Fig. 7.11**), drops to the ground, and pupates. Relatively dry pasture is necessary for pupal survival, this being a limiting factor in the fly's distribution. On the other hand they are resistant to low temperature (–20°C), and in this connection note they are found as far north as 60°.

Ovipositing flies cause the cattle to 'gad about': they may even run into fences in their evasive efforts or, with surprising intelligence, stand in any available water to avoid oviposition. These behaviours cause varying degrees of stress and results in reduced milk yield, loss of weight and the abortion of calves. The larval damage is even greater than this, for not only may the mobile larvae render the meat unsaleable, but also the hide is partly destroyed by the holes above the warbles. The larvae in their various movements within the body sometimes lose their way, ending up in other organs, and when this site is the brain partial paralysis results.

The old-fashioned control method is to squeeze out the warbles manually. A co-ordinated effort to do this in Cyprus resulted in the extinction of the fly there. Insecticides may be used to treat the cattle topically along the midline of the back, or systemics such as famphur (Warbex®) and fenthion may be applied externally to non-lactating cattle. They are designed to kill the young larvae. More recently macrolide antibiotics such as ivermectins (e.g. Ivomec®) have been used. These kill not only the young migrants but also the larvae in the warbles. SMT cannot be used as the flies cannot be cultured. Research is continuing to develop vaccines. As our control of these flies tightens, indeed they are extinct in much of Europe, they have begun to explore new hosts. Cattle farmers are mainly affected, often in the neck region, causing partial or total paralysis. Ocular myiasis has also been recorded in which an eye is lost. Both *H. bovis* and *H. lineatum* are involved.

Wild deer are attacked by *H. diana* and *H. actaeon*. In northern Europe reindeer host *Oedemagena* (= *Hypoderma*) *tarandi*. The status of a sixth species, *H. sinense*, has been confirmed by molecular techniques (Otranto *et al*., 2005). It attacks cattle and yaks in China. *Crivellia silenus*, the goat warble fly, is distributed in North Africa and warm-temperate Eurasia.

7.4.1.1(d) DIPTERA; CYCLORRHAPHA; Oestridae; Cuterebrinae. *Dermatobia hominis*. Human bot. A Neotropical fly attacking people and livestock. August Busck (1912) gave a detailed account of the deliberate rearing of this bot in his own arm, hence showing considerable scientific commitment. The fly is found from 18°S to 25°N and favours moderate altitudes and moist, forest conditions, such as coffee growing areas in Columbia and Nicaragua. It is an attractive metallic blue with yellow legs. Like *Wohlfahrtia* (Section **7.4.1.2(c)**) it attacks people and livestock, but is peculiar in not laying eggs directly on the host. Instead, females attach eggs to Diptera in flight, often mosquitoes or muscid flies associated with mammals. Fecundity reaches ~800–1000 eggs. Pharate larvae develop within the protective chorion until they may be stimulated to escape by the body heat of a potential mammalian host. Since development takes ~6 days, many of these phoretic beasts and their egg burden will perish in the interim. But it is startling to realize that a mosquito injecting you with *Plasmodium falciparum* (Section **7.3.2.4(d)**) may be depositing a *Dermatobia* larva at the same time! The larva bores your skin and reaches a length of ~2.5 cm producing a painful, boil-like swelling. Larval development takes 6–12 weeks and like other flies causing myiasis pupation is in the ground. While *D. hominis* is still confined to the Americas, it has the potential to reach other continents in infected people or cattle, especially because of the extended period of larval development.

7.4.1.2(a) DIPTERA; CYCLORRHAPHA; Calliphoridae. *Auchmeromyia senegalensis* (= *luteola*). Congo floor maggot. An anomalous, sub-Saharan blood sucker. Both this and the next species are found in and around huts and houses in tropical Africa, where the adults feed on faeces and rotting fruit. The females lay several batches of ~50 eggs on the ground. The larvae, which hatch in a few days, suck the blood of people sleeping there by making an incision with their mouth hooks. They take a 20 minute blood meal every few days and also feed on wild mammals such as warthogs and aardvarks. Since the larvae cannot climb the legs of a bed, this simple device provides total protection.

7.4.1.2(b) DIPTERA; CYCLORRHAPHA; Calliphoridae. *Cordylobia anthropophaga*. Tumbu fly. A human bot fly from Tropical Africa. Like tsetse, the adults prefer shaded situations where they lay batches of 100–300 eggs in the sand, particularly if it has been contaminated with urine and faeces. But they will also lay eggs on soiled clothes. The first larval instars respond positively to heat, CO_2 concentration and, like fleas, to vibration, as a means of locating hosts. They can penetrate human and mammalian skin in less than a minute, producing boil-like swellings. After ~8 days of larval development they escape and pupate in the soil. *Cordylobia rodhaini* is a rarer but similar species.

7.4.1.2(c) DIPTERA; CYCLORRHAPHA; Calliphoridae; Sarcophaginae. *Wohlfahrtia magnifica*. A bot causing wound myiasis of people and livestock in arid regions of Asia and Africa. The Sarcophaginae or flesh flies, which are sometimes regarded as a separate family, are rather large, grey, tessellated flies that are common on carrion. But this brute causes obligate myiasis of people and livestock in mainly arid regions of North Africa, Asia and sometimes Europe. It is active only in warm, bright weather when females larviposit directly into any cuts and abrasions. Fecundity according to female size is ~100–200. Rarely, larvae have been deposited in human ears or noses, with horrific results. Pupation is in the soil and in cooler regions they overwinter as diapausing pupae. *Wohlfahrtia vigil* is a North American species found from Alaska to Pennsylvania. The young larvae can penetrate only delicate human skin, such as that on infants. Occasionally the larvae of *Sarcophaga* spp., such as *S. haemorrhoidalis*, are found in human wounds.

7.4.1.2(d) DIPTERA; CYCLORRHAPHA; Calliphoridae. New World Bots. *Cochliomyia* (= *Callitroga*) *hominivorax*; *C. macellaria*. Primary screw-worm and secondary screw-worm. Bots of livestock and occasionally of people, subsequently found in North Africa. *Cochliomyia hominivorax* is Neotropical and formerly penetrated warmer regions of North America in the summer. Individual females can migrate up to ~300 km (Hightower *et al*., 1965) and there were seasonal population movements from Texas to Oklahoma in the USA. But the species cannot survive winter in these regions.

The SMT was applied successfully to this species in Curaçao in the 1950s, an island sufficiently small to test the method's feasibility (Baumhover *et al.*, 1955). By 1960 SMT had eliminated this fly from Florida at a cost of US$11 million; SMT was used to eradicate it from the USA and Mexico by 1991 (US$750 million), much of Central America (Myers *et al.*, 1998b) and the Caribbean. The annual cost to stop re-invasion of the USA is US$35 million. In Jamaica, a recently introduced SMT programme has still to be completed. In 1988, *C. hominivorax* was found in Libya, having arrived in goats transported from South America (Hill, 1997). There it rapidly infested some 200 people and 2000 domesticated mammals, mainly sheep. In 1990, >12,000 cases of myiasis were reported. The fly was eradicated by 1991 using sterile males from Mexico at a rate of up to 40 million per week, along with other techniques (Lindquist *et al.*, 1992) at a total cost of some US$64 million, rather more than the value of the goats.

The biology of the fly is similar to that of *Lucilia*, given below. Adult females oviposit several hundred eggs in wounds on mammals, achieved fecundity often being >2000. Their rapidly developing larvae feed directly on the living tissue and on tissue exudates. The result has been termed, aptly, *traumatic myiasis*. Under optimal conditions the life cycle is ~20 days. Much of the screw-worm population exists in the wounds of wild mammals, thus forming a natural reservoir population (Section **13.1.2.2**). In rare cases people who have been knocked unconscious for an extended period, for example, in a car accident in an isolated place, have been attacked, resulting in hideous facial disfigurement. It has also caused vaginal myiasis in tropical hospitals. Olfactory cues from infected mammals attract additional flies, including *Cochliomyia macellaria*. This fly can rapidly cover distances of ~10 km/day, so that large numbers may congregate rapidly. It oviposits on carcasses but also lays eggs on victims already infested by its congener. So, *C. hominivorax* is primary and *C. macellaria* secondary.

7.4.1.2(e) DIPTERA; CYCLORRHAPHA; Calliphoridae. *Chrysomya bezziana*. An Old World bot with biofacies similar to *Cochliomyia*. This species is distributed throughout the Old World tropics and sub-tropics: Africa, India, much of South-East Asia and China to Indonesia, the Philippines and New Guinea. Females lay 150–500 eggs in wounds and scratches and on mucous membranes. The larvae, feeding *en masse*, complete development in 5–6 days, then pupate in the ground; adults emerge in warm weather some 8 days later, but may take several weeks in cooler regions. It is especially important in India, often causing human myiasis, but cattle, sheep and goats are also afflicted. Because the adult flies feed on carcasses and faeces they may mechanically transmit pathogenic microorganisms. Perhaps with the economic growth of India, China and South-East Asia, generally it may soon be feasible to use SMT to eradicate these flies. As with *C. hominivorax*, other species of Old World *Chrysomya* exist that cause facultative myiasis, including *C. megacephala* and *C. albiceps*. The latter species is an aggressive predator of other blow fly larvae in carrion (Del Bianco Faria *et al.*, 1999), who conjecture that its recent introduction into the Americas has caused the numbers of *C. macellaria* to decline.

7.4.2 Facultative myiasis

7.4.2.1(a) DIPTERA; CYCLORRHAPHA; Calliphoridae. *Lucilia* (= *Phaenicia*) *cuprina*, *L. sericata, Calliphora stygia*. Sheep strike flies; green and blue bottles. *Lucilia* species are rather similar morphologically and were often confounded in early work, creating confusion (Section **1.4.4**). Both these species oviposit on fresh carcasses or on the wet or wounded areas of living sheep. But *L. sericata* also oviposits on old cadavers. They lay 2000–3000 eggs, usually in batches of 200–250. Kairomones emanating from the dermatitis caused by the fleece-rot bacterium *Pseudomonas aeruginosa* attract *L. cuprina* and only this fly can maintain itself alone on a sheep. *Lucilia sericata* oviposits on live sheep only after *L. cuprina* has done so and needs the presence of its congener to maintain it. In the absence of carrion only *L. cuprina* persists; in the absence of sheep only *L. sericata* persists (Andrewartha and Birch, 1984). A third species, *L. caesar,* breeds in carcasses and dung and is also cosmopolitan.

Far from sheep-rearing areas, blow flies are often more numerous in urban situations, where they feed on badly disposed of waste food, than they are in the country. Urban flies migrate to farms and cause strike (Green and Kane, 1954). They can live for 3–4 weeks and travel several kilometres in a day, flying near the ground. 'Greenbottles', probably *Lucilia* spp., are recorded in numbers flying onto an oilrig 130 km off the Australian coast (Bye, personal communication, 2016). In a study on insect biodiversity I did in 1996–1998 throughout England, calliphorid flies (*Lucilia* and *Calliphora* spp.) were more common in urban woodlands than in rural ones.

Lucilia cuprina is more numerous in the Southern Hemisphere while *L. sericata* is found more to the north, but there is quite a lot of overlap. In Australia and South Africa, 90% of sheep strike is by *L. cuprina*. The eggs, which are often laid on the shaded areas of the victim, hatch within a day. Larval development may take less than a week on living mammals, whose body heat doubtlessly contributes to this rapid rate. The pupal stage takes only ~8 days, although larval diapause may occur in *L. sericata*. Larvae about to pupate move far from the feeding site, as in many caterpillars, thereby reducing population density. But in most cases metamorphosis is short for a temperate insect, and comparable to that of the house fly.

Such potential for a rapid build-up of population underscores the serious effect that these flies may have, should they oviposit on living sheep. The dispersive ability of *Lucilia* spp. and their attraction to livestock means that they are a constant hazard to sheep during the warm months of the year, especially in sheltered, damp locations. Facultative myiasis allows the flies to buildup numbers away from the stock in a parallel path not open to those causing obligate myiasis. While lambing is an early springtime event, still-born lambs, or young lambs which die, become a vast food source for *Lucilia* if they are not deeply buried or burnt, especially as the weather warms up. Although secondary flies in carrion may kill a majority of *Lucilia* in many situations I have seen large numbers of them emerging from around lamb carcasses in Kent. Then I had a recent conversation with Jack Joyce in Connemara, Ireland, a sheep farmer of insight, but even so he was unaware of this association after 40 years of farming. Those of us with entomological training will be surprised, but it shows that as applied entomologists we must endeavour to put ourselves in the farmer's place. Clad in boots and Mac on a cold, wet, blustery night in March when you are helping ewes to lamb entomology is not in your mind!

Attack sites are often lesions on adult sheep resulting from contact with fences, especially barbed wire, or fighting in rams. Bites from *Ixodes* ticks or sheep keds (Section **7.2.2.1**) may also attract oviposition. But egg laying also occurs on undamaged sheep in the area of the breach, especially in wet weather if the fleece is long or feculent. Merino sheep are especially vulnerable. In the Mules' operation, which is generally performed on Australian merinos, the loose skin in the breach is removed surgically. This reduces strike by 80–90%. The operation was started in 1931, but was suspended with the advent of organochlorine insecticides. It was introduced again in the 1970s when insecticidal control began to fail. In New Zealand, strike is far more of a problem on the warmer North Island, where most of it is caused by *Calliphora stygia*. Here the breach is routinely clipped 6 months after shearing to remove feculent wool, locally termed 'dags'. Because the progress of attack is rapid, so that the term 'strike' is apt, a daily watch must be kept over the flock, but while this is easy on fenced animals on lowland pasture, upland and range sheep are, of course, much less easy to monitor. The behaviour of struck sheep gives a clue as to their condition. They normally wander away from the rest of the flock, lay down and do not feed. Undetected struck sheep suffer a rapid but awful death and their carcasses provide a further source of food for the expanding *Lucilia* population, until secondary flies move in, rather like jackals.

7.4.2.1(b) DIPTERA; CYCLORRHAPHA; Calliphoridae. *Calliphora vicina* (= *erythrocephala*), *C. vomitoria*, *Chrysomya rufifacies* and *Ch. albiceps*. Secondary strike flies. There are also tertiary flies such as *Musca* spp. (Section **7.4.2.1(c)**). Fortunately for farmers, competitive and even predatory interactions with these secondary flies often lead to high mortality of *Lucilia,* and mammalian and avian scavengers will often destroy both the carcasses and the flies they contain (Putnam, 1977). In the Australian summer, *Chrysomya rufifacies* often becomes so numerous that, due to competition and predation, the numbers of *Lucilia* emerging from carcasses are low (Andrewartha and Birch, 1954). In South Africa, there are five common species of *Chrysomya* (Richards *et al.*, 2009). In Europe, the braconid wasp *Alysia manducator* parasitizes carrion flies. Other calliphorid genera with proclivities for carrion include *Cynomyia*, *Onesia* and *Pollenia*, but *P. rudis* is an earthworm parasite (Colyer and Hammond, 1951).

7.4.2.1(c) DIPTERA; CYCLORRHAPHA; Muscidae. *Musca domestica, M. autumnalis, M. vetustissima* and *M. sorbens*. House flies, face flies, bush flies and bazaar flies. Nuisance flies that also cause tertiary myiasis and spread disease by contamination. Although these ubiquitous beasts (*Musca* has >60 Old World species; Krafsur and Moon, 1997) may be involved in tertiary myiasis, and can be placed here for that reason, they may have other more serious effects on our lives and those of our domesticated animals. As a group they are cosmopolitan, but form denser populations in some parts of the world (e.g. North Africa and Australia) than in others. Because they are so familiar to us, their importance as a hazard to health is often neglected. Their mechanical transfer of faeces to food can spread anthrax, cholera, *Shigella*, the organism causing bacterial dysentery, and typhoid fever. With *Stomoxys calcitrans* and *Hydrotaea aenescens,* they transmit enteric diseases including those caused by *Campylobacter* and haemorrhagic colitis caused by *Escherichia coli*. With *Calliphora* and *Lucilia,* they may spread *Mycobacterium avium* subsp. *paratuberculosis*, which causes paratuberculosis in ruminants. *Musca sorbens*, *M. lineata* and *M. planiceps*, using peristomal teeth on their mouthparts, can open wound scars and may suck blood. *Musca sorbens* transmits the bacterium *Chlamydia trachomatis*, which can result in blindness. *Musca autumnalis* transmits the eubacterium *Moraxella bovis* causing bovine pink eye, and also several species of the spirurid nematode *Thelazia* (Krafsur and Moon, 1997). Another nematode, the widespread *Parafilaria bovicola*, develops in the fly's haemocoel. It produces dermal lesions on which the flies feed, thus infecting themselves, and causes green-muscle disease in cattle, rendering the carcasses unsaleable. In all, more than 100 pathogens are recorded from house flies, of which ~65 are known to be transmitted (Service, 2000).

Many *Musca* spp. are capable of dispersing themselves, and the diseases they may carry, several kilometres in the space of a few days (see Table 31 in Johnson, 1969). *Musca autumnalis*, following its arrival in Nova Scotia, Canada, in the late 1940s, spread across North America to Oregon, USA, at a rate of 200–300 km/annum (Krafsur and Moon, 1997). The Australian bush fly *M. vetustissima* has become particularly numerous because it breeds in cattle and sheep dung and is capable of lengthy migrations.

In cool climates, house flies spend the winter in the puparium, but even this stage is not very cold hardy (Coulson and Bale, 1990), so, cold winters are inimical to them. Other stages may occur at this time only in warm micro-environments and these are generally associated with people. *Musca autumnalis*, however, overwinters as a pre-reproductive adult. But in both flies, overwintering is critically dependent on finding physically favourable sites. Newly emerged *M. domestica* take some time to mature, but surviving females lay several batches of >100 eggs on faeces and other damp organic waste, in all >500 may be laid. The eggs are very sensitive to harsh conditions and killed by dryness, and temperatures >40°C and <15°C (Service, 2000). *Musca autumnalis*, together with *Haematobia irritans*, is one of the first species to oviposit on fresh cow dung. Development is rapid: from 10 days under ideal conditions to more typically 3–4 weeks in temperate conditions. Prior to pupation the larvae disperse from the feeding site, so greatly reducing their population density (Service, 2000; Section **10.2.1**). One appreciates that the reproductive potential of these pests is very great under conditions favourable to oviposition and survival. In Jamaica, the association of high fly numbers with the rains and with the mango season is well known, while in dry periods house flies are blessedly scarce.

Several other cyclorrhaphan flies may be involved in facultative myiasis. These include *Fannia* and *Muscina* (Muscidae) and *Chrysomya*, *Phormia*, *Cynomyopsis* and *Sarcophaga* (Calliphoridae). *Fannia pusio* breeds in chicken dung. The pteromalid wasps *Nasonia* (= *Mormoniella*) *vitripennis, Muscidifurax* spp. and *Spalangia* spp. parasitize the puparia of many of these muscid and calliphorid flies (Section **7.3.2.4(o)**). In Denmark, *S. cameroni* has been used experimentally, and with some success, for reducing the density of *M. domestica* on cattle and pig farms (Skovgård and Nachman, 2004). Rates of parasitism increase at higher temperatures. Other larval/pupal parasitoids of these flies are *Aphaereta pallipes* (Braconidae), *Eucoila* sp. (Cynipidae), *Xyalophora quinquelineata* (Figitidae) and the peculiar staphylinid parasitoid *Aleochara* (Section **8.2.2.4(d)**). As with mosquitoes, exclusion by screening windows and using fans, plastic strips or curtains in doorways can reduce but not eliminate the fly problem. Again, denying breeding sites by proper waste disposal is essential. Old-fashioned sticky flypapers are remarkably effective within buildings, but these beasts have become resistant not only to DDT but also to OPs, carbamates and pyrethroids. *Bti* is often used to kill both larvae and adults.

8 Beneficial Insects

8.1 Introduction

So far we have considered the negative side of insects, but there are many positive sides, for they may be beneficial to the environment in general, to plants and to ourselves (Metcalf and Metcalf, 1993). What constitutes being beneficial, however, is debatable. What is beneficial to us is pretty clear, as there is a single, anthropocentric view, for example the pollination of crops (Free, 1993) and the use of parasitoids in biological control. But what is beneficial to the general environment is harder to assess because of the interwoven nature of the ecological web (Andrewartha and Birch, 1984). For example, caterpillars browsing in a forest deprive trees of some photosynthetic area but their dead bodies and falling faeces add to soil fertility beneath, and their adults may be pollinators. When aphids feed on a large linden tree (*Tilia*), up to 1 kg/m^2/yr of honeydew is produced. This contains both sugars and amino acids. Some falls on the soil, often after rainfall, and so may improve nitrogen fixation and soil fertility (Owen, 1980). But much is held on leaf surfaces, providing food for other insects and a complex microflora, only to reach the soil after leaf abscission. Nutrient cycling is augmented, but the trees are net losers (Choudhury, 1985). Then, predation is often cited as improving the race as 'only the strong survive'. While we will concentrate on those insects that are directly or indirectly beneficial to us, paying particular attention to pollinators and those groups of predators and parasitoids that are used in biocontrol, we also consider some of the ways in which insects benefit the general environment.

Insects exert major influences in ecological processes in terrestrial and freshwater environments. They function as soil formers, as pollinators and protectors of flowering plants, especially fruit crops and vegetables, and as enemies of other insects, thereby being a major reason why so few such populations become epidemic (Section **9.4**). As prey, they are food for a wide range of other organisms, such as spiders, amphibians, reptiles, birds and mammals. Insects also influence the numbers of many plant species and we have used them to control weeds. These are significant relationships in the ecological web and hence in agriculture and forestry. In addition, insects have helped us to develop biological science, not only entomology itself but also genetics, taxonomy, physiology, ecology, behaviour and evolution. Early in the twentieth century, T.H. Morgan (see **Fig. 11.4**) used the fruit fly *Drosophila* to verify and extend Mendelian principles to the animal kingdom, thereby confirming the genetic basis of biological inheritance. Today, thousands of people work on *Drosophila* because, apart from its ease of handling, compared to us its genetic similarities are greater than its genetic differences. Put simply, over 70% of this fly's genes are common with ours, showing the conservative nature of genetical systems and the biochemical pathways they control. In ecology, much of the theory of animal numbers was developed by entomologists (Section **11.1**). A further fascinating if gruesome area in which insects are used is forensic science (Section **8.3.1**). But although there are some insect products, compared with those of vertebrates they form a disappointing array: for example, only silks, honey, some waxes, shellac and cochineal are of much importance.

Finally, some insects have great beauty, not only the static attractiveness of insects pinned in a collection, but also the dynamic beauty of the living animal. Naturally, butterflies and moths spring to mind, but others such as dragonflies, some bees and wasps and a few Diptera like big assassin flies are impressive and may have astoundingly complex behaviour. One of the great founders of American entomology was J.H. Comstock. Here he waxes lyrical on the splendour of his favourite hawk moths (Comstock, 1940):

> Of all the beautifully arrayed Lepidoptera some of the hawk moths are the most truly elegant. There is a high-bred tailor-made air about their clear-cut

> wings, their closely fitted scales and their quiet but exquisite colors. The harmony of the combined hues of olive and tan, ochre and brown, black and yellow and greys of every conceivable shade, with touches here and there of rose color, is a perpetual joy to the artistic eye.

But my favourites are the orchid bees, those vibrant miracles of miniaturization zooming with intent through Neotropical rain forest (Section **8.3.6**).

8.2 Insects in Ecological Processes

Insects are by a huge factor the dominant terrestrial life form not only in terms of the number of species and individuals, but also in biomass. With probably more than five million species (Hammond, 1992; Hammond, personal communication, 2005) they vastly outnumber the land vertebrates, which have <20,000 species. The number of individuals of a pest species often exceeds 1 million/ha. They comprise a major part of the terrestrial animal biomass, often in excess of 10 kg/ha and, with the exception of mammals of the East African savannah, one normally greater than that of resident vertebrates. They thereby exert a considerable, although often cryptic, influence in such ecosystems, particularly community energetics and in recycling nutrients, as their metabolic rates can be relatively high. Agriculture and forestry reshape these processes for production, employment and profit.

8.2.1 Pollinators and protectors: Trends in co-evolution?

We deal here mainly with beneficial insects such as pollinators, but in Section **8.2.3** mention a few that attack weeds and so are beneficial to us. Plants attract insects when it is to their individual advantage (e.g. pollination) but seek to repel them when it is not (e.g. herbivory; Section **2.4.2**). While evolution continues, in response to changes in the physical and biotic environments (Haldane, 1954), that in response to interacting organisms, the memorable Red Queen hypothesis (Van Valen, 1973), which has its origin in Fisher's (1930) work, may lead to co-evolution (Cott, 1940; Ehrlich and Raven, 1964; Mitter *et al*., 1991), although not to any tangible advance (Wright, 1982a, b). Janzen (1980) says: 'Coevolution …[is] an evolutionary change in a trait in the individuals of one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first'. Or more succinctly, as: 'reciprocal evolutionary change in interacting species' (Thompson, 1982), involving mutual selective pressures. Co-evolution is continuing, positive, negative or neutral for each interactant (Vinson, 1984), giving nine possible outcomes for a given pair (Mattson and Addy, 1975). But if one of the interacting species is replaced by another, a process continues that is not entirely co-evolved (Janzen, 1980): a ghost of co-evolution past (Section **11.5.2.2**). The primary requirement for co-evolution is co-occurrence (Connell, 1980). It does not proceed in 'a spaceless arena'; spatial relations of the interactants are paramount. Since interacting species comprise genetically different populations, differ in their spatial distribution, and because the outcomes vary between habitats (Thompson, 1997), co-evolution is complex. If the interaction is confined to a species pair, co-evolution is *tight* and specific; if a species assembly is involved this process is *diffuse* (Levin, 1992). For the latter, the mutual interactions between plants, their pollinators and the animals that transport their seeds have greatly enhanced the Earth's biodiversity (Bascompte *et al*., 2006), which we are busily destroying (see van Swaay *et al*., 2006).

But how important may co-evolution be in plant–insect interactions, especially those with herbivores? Few insect populations impose significant selection pressures on their food plants (Strong *et al*., 1984), who say that '… the known examples of coevolution look increasingly like small vortices in the mainstream of evolution'. It may be confined to simple interactions as when a few monophagous or oligophagous species feed on short-lived, scattered plants. One cannot imagine co-evolution between, say, oak trees and each of the myriad insect species that feed on them. And as with competition (Connell, 1980) the residual results of past co-evolution could remain. The insect fauna on plants '… is a *pot pourri* of the coevolved, the pre-adapted and the opportunistic in varied and unpredictable proportions'. Many orthopteroids and the larvae of noctuid moths eat a heterogeneous collection of plants, see also Jermy (1984). Co-evolution fails to provide a general mechanism to explain the present structure of such insect faunas (Strong *et al*., 1984). Even so, Mitter *et al*. (1991) remind us that much more work must be done for a more comprehensive conclusion.

Simplistically, however, the evolutionary outcomes of interactions between separate species, whether plant or animal (Section **10.1.2**), may be regarded as advantageous (+) or disadvantageous (–) for each individual. So we have (+ +) interactions such as mutualism, (+ –) interactions of enemy and victim, or (– –) interactions that can be the result of competition. There are also neutral interactions, (o o). Putting these outcomes on a graded scale, there will be asymmetrical effects if one party affects the other more than vice versa (Bascompte *et al*., 2006). While pollination and the mutual protection afforded between plants and some insects come in the (+ +) category (Bronstein, 1998), as in human friendship there is a tendency for individuals to maximize their ratio of benefit to cost (Dawkins, 1989), perhaps resulting in conflict (Willmer and Stone, 1997).

While the flowers of some plants resemble those of others, there being Batesian and Müllerian types (Dafni, 1984; Section **10.2.3.5**), we are concerned mainly with relationships between *insects and plants*. Many orchid species get themselves pollinated by deception (Dafni, 1984; Dettner and Liepert, 1994; Cozzolino and Widmer, 2005; Schaefer and Ruxton, 2009; Trivers, 2011; Section **10.1**). Flowers may have no nectar, a feature encouraging a short stay on the plant and hence outcrossing. Then, like *Ophrys* and *Chiloglottis*, they may deceive male bees that flowers are conspecific females (*pseudocopulation*), or are potential hosts for parasitoids (*pseudoparasitism*), or may elicit territorial defence (*pseudantagonism*). The flowers of *Scoliopus bigelovii* mimic basidiomycete fruiting bodies both in appearance and odour, and are pollinated by fungus gnats (Mycetophilidae) (Fenster *et al*., 2004). Blood-sucking Diptera, duped by CO_2 and heat production (Section **7.3.1.1**), pollinate *Arum conophalloides* (Knoll, 1926, in Dafni, 1984). But such interactions are not always in the plant's favour. Carpenter bees (*Xylocopa*) rob nectar though the base of a flower, performing no benefit to the plant (Raw, personal communication, 1975). Even so, some nectar-robbing *Bombus* still pollinate many of the plants they visit.

Several British species of *Hadena* (Noctuidae) are associated with campions (*Silene*, Caryophyllaceae; South, 1920/1923). *Hadena caesia* is found on *S. maritima*, *H. conspersa* on *S. noctiflora*, and *H. albimacula* on *S. nutans*. *Hadena bicruris* is a specialist pollinator of *Silene latifolia alba* and *S. dioica* (Bopp and Gottsberger, 2004). But it also oviposits in the fertilized flower and its larvae consume the developing seeds. Plate 130 in South (1920/1923) shows a larva, squirrel-like, holding a seed that it is gnawing. Like relationships are infrequent, however, but occur between *Yucca* plants and *Tegiticula* moths (Riley, 1892, in Baker, 1961), *Trollius* flowers and *Chiastocheta* flies, and *Lophocereus* cacti and *Upiga virescens* moths (Holland and Fleming, 1999). Deception arises since the evolutionary interests of the parties are at variance. In the *Lophocereus*/*Upiga* case the plant responds by aborting some of the infected seed, an option that plants often employ. A similar but intraspecific divergence of evolutionary interest occurs in parent/offspring conflict (Trivers, 1974), which includes the special case of insectan dispersive behaviour (Section **10.2.4.1**; Starrfelt and Kokko, 2010).

8.2.1.1 Pollinators

The great majority of Angiosperms employ cross-pollination (Real, 1983), which is essentially genetic dispersal between bisexual flowers. Unlike fertilization in insects, mating partners in these plants are not necessarily in close proximity. The male sex cells (pollen) of one plant must be transferred to the female part (style) of another in order to effect fertilization, although in default many can self-fertilize, or are adapted for regular self-fertilization (Takhtajan, 1969; Cronquist, 1988). Baker's Rule states that self-fertilizing plants are better initial colonists, since conspecific pollen may be scarce or absent in such situations. Compare this to the Allee effect (Section **10.2.2.4**) for animals, to vagrant, parthenogenetic aphids and groups colonizing new crops. Flowers that self-fertilize are generally small, inconspicuous and may not even open. Attraction is unnecessary.

Since flowering plants do not, of course, move themselves, to be cross-pollinated they must employ a mobile agent. In Gymnosperms, (pines, firs and their relatives) and in several groups of Angiosperms, wind is the agent, a system called *anemophily*. Gymnosperms often live in cold and/or extreme environments. Unlike insect pollination, called *entomophily*, wind pollination can proceed in inclement conditions. But it is a chancy business requiring much pollen, whose advective dispersal is affected by wind speed, diffusion due to its turbulence and gravity. Effective anemophily is restricted to an ambit of <50 m (Colwell, 1951, in Ehrlich and Raven, 1969). As pollen is often protein rich (2.5–60%; Roulston and Cane, 2000, in Wäckers *et al*., 2007) and usable nitrogen to synthesize it may be scarce (Mattson, 1980b; White, 1993), anemophily can drain the plant's metabolic resources that might, with a more cost-effective reproductive strategy, be used for growth and protection. But anemophily may not be the primitive condition, as Darwin believed (Cox, 1991). In conifers the cone itself is an evolved aerodynamic structure that stalls conspecific pollen in particular, and directs it to the ovules (Niklas, 1985). Similarly, spikelets of grasses oscillating in the breeze are often specialized pollen-capturing organs. Even so, wind pollinated plants cannot be rare as entomophilic ones can be (Knoll, 1986).

Flowering plants are commonly symbiotic with a variety of insectan pollinators, the flower being the evolved device to attract them, to receive pollen from them and to dispense pollen to them (Faegri and van der Pijl, 1978; Barth, 1991). While this strategy costs the plant in producing the often highly visible flower, the floral scent and often nutritional rewards for the pollinator, it requires less pollen. Notable exceptions in Angiosperms are anemophilous grasses (including grain crops), rushes and catkin-bearing trees like oaks, hazel and willows. In this case many conspecific plants usually grow close to each other, thus making anemophily less inefficient.

The size and mobility of many insects, especially with those having high individual searching capacity (ISC; Section **10.2.4.1**), make them likely evolutionary candidates for moving pollen (Kevan and Baker, 1983), and while some birds and mammals also pollinate, being generally larger, they are better pre-adapted for seed transport (Regal, 1977). Some insect species move pollen many kilometres when migrating. Because pollen grains are very durable and often highly specific to a given plant, pollinators often 'self-mark', either on their bodies and/or within their guts. Using this fact, Wratten *et al.* (2003) were able to study the movement of several species of hover flies.

While all cereal crops are anemophilous, over 90% of Angiosperms are pollinated by animals, namely *zoophily* (Strong *et al.*, 1984), the monetary value of this global service being estimated at ~US$200 billion (Reynolds, 2012b). But recent intensification of farming has led to a decline in the numbers and variety of insectan pollinators (Kremen *et al.*, 2002; Klein *et al.*, 2007; Garibaldi *et al.*, 2013). Of course, co-adaptation is generally at work here so that the size (Greenleaf *et al.*, 2007) and many other features of both pollinator and flower are indeed co-evolved (Section **8.2.1**). This leads to the evolution of a *pollination syndrome* (Faegri and van der Pijl, 1978; Fenster *et al.*, 2004). We recognize a suite of related pollinators, for example large bees with long tongues co-adapted with specialized flowers. Here, competition (Section **9.8**) may ensue between plants for pollinators and between pollinators for floral resources. Apart from these relationships we recall that some bees rob resources from plants. For the Hymenoptera, note that while flowers attract bees and others by their visibility, potential victims of aggressive wasps have evolved to be inconspicuous.

In the beginning, Permian fossils show that insects such as Psocoptera were eating pollen. Indeed, pollen and spore eating preceded other forms of phytophagy (Southwood, 1985; Scott *et al.*, 1992). Collembola may have moved microspores as early as the Devonian (Kevan and Baker, 1983). The Permian palaeodictyopteran *Goldenbergia* may have fed on the big pendulous cones of lycopods (Brodsky, 1994). Today the ancient cycads (dating back 250 million years ago [Ma]) still attract insects by the pollen itself in massive cones, an expensive commitment to reproduction. The first flowers did not originate with the Angiosperms, however, but about 225 Ma with the Bennettitales, an early offshoot of the Gymnosperms, now extinct. Bisexual flowers were found at this time so that when pollen-eating insects moved between them, unrelated pollen was transported near to the ovary. Primitive extant Angiosperms such as magnolias and water lilies did not appear until the late Cretaceous some 135 Ma, while bees came much later, a mere 30 Ma, so as pollinators they are successful new girls on the block (~25,000 described species). Bilaterally symmetrical or *zygomorphic* flowers, as in the Labiatae, Papilionaceae and Orchidaceae, have most likely evolved to facilitate pollination by them.

Through evolutionary time, flowering plants pollinated by flying insects have substituted sugary nectar (containing sucrose, glucose and fructose) as bait instead of copious pollen, conserving nitrogen and providing fuel for these active agents (Kevan and Baker, 1983). A foraging honeybee (*Apis mellifera*) consumes sugar at a rate of 4–10 mg/h (Wigglesworth, 1984), which is >10% of its live body mass. Bumble bees (*Bombus*) are similar. Much of their flight is hovering, a very expensive activity (Kammer and Heinrich, 1978), while lift from hovering is even more energetic (Dudley, 1995). But plants must not provide too much fuel as this would reduce the number of flowers visited per trip, and so the chance of outcrossing. Most pollinators (bees, syrphid flies, heliconine butterflies) collect or eat pollen and their frass may still contain it, giving us a clue as to their movements. Many plants donate amino acids to the nectar (Baker and Baker, 1973; Kevan and Baker, 1983). Surveying 395 plants they found 20 amino acids in nectar, many essential to a bee's metabolism. These also enhance the achieved fecundity (AF) of pollinating butterflies (Cahenzli and Erhardt, 2013). So flowers provide a major source of food for visiting insects. Both scent and colour are used to attract them, a system allowing unseen flowers to be found. Floral scents are complex (Raguso, 2009) and best viewed in the totality of chemosensory relationships between whole plants, their pollinators and their enemies (Strauss and Armbruster, 1997). Over 1700 volatile organic compounds have been identified, but limonene and benzyl alcohol are common components. In trials, chemical attraction via volatiles may override that from vision (Hambäck, 2015). Pollinators also monitor floral CO_2 levels (Thom *et al*., 2004; Guerenstein and Hildebrand, 2008). In many Lepidoptera, receptor cells on the labial palps detect elevated CO_2 near flowers. Insects in general live in a highly chemosensory world, just as we, with our limited sense of smell, live in a highly visual one.

Entomophily, then, permits greater efficiency of pollen dissemination than does anemophily: the wind blows in but one direction at any time but pollinating bees and flies can fly potentially in any direction in their search for flowers. Nor is pollen lost constantly by gravitation (Okubo and Levin, 1989), or by sticking to damp leaves and other objects. Moreover, some flowers have evolved to resist access by undesirables. But persistent low temperature and windy conditions reduce insect activity and apart from some specialized, heterothermic bees such as *Bombus*, few pollinators can fly in such weather. This may explain why many trees in cool temperate regions and more so in the taiga are anemophilous. Another problem for entomophilous trees is that, being so large, their possessing numerous flowers per plant does not make for efficient cross-pollination (Heinrich, 1975). Most plants, however, have intrinsic mechanisms to resist self-fertilization (Brewbaker, 1957; Charlesworth, 2000; Li and Newbigin, 2002), the style being the floral organ that selects male gametes.

Floral structure and the time of opening restrict the type of insect that can obtain access to the nectaries and often to the pollen. Such control by the plant is necessary because not all insects are capable of achieving efficient cross-pollination, critically, high *floral constancy*. Ideally, a plant needs to receive only conspecific pollen and to donate its pollen only to conspecific plants. Unsuitable visitors merely consume or waste the valuable products. Indeed, the long history of co-evolution between flowering plants and their insect pollinators has resulted in much of the great variety of floral types that most people take for granted. Insect pollinators are ultimately responsible for much of the beauty of flowers that we enjoy. Without them there could be no Chelsea Flower Show! Why we think flowers are beautiful is yet another matter.

Flowers are often born in clusters, or *inflorescences* of various types functioning as large attractive (*apparent*; Section **2.4.2**) masses for pollinators and may provide a landing platform, as in the Umbelliferae. They also allow production of a multiplicity of small seeds, offsetting the hazards of distribution and germination. Seed production in plants follows many similar rules to those of egg production in insects. Seeds are either small and numerous, as in Compositae, or few and large, as in coconuts. In the former, parental investment favours the parents, in the latter it favours the offspring. In a few tropical trees, the so-called 'cornucopian species', like *Jacaranda mimosifolia,* and *Trabebuia rufescens* (Bignoniaceae), the whole plant becomes a mass of blossom before the leaves develop, in effect one gorgeous inflorescence. While this must be at a great metabolic cost, it is presumably offset by attracting bees from a wide area. Fast-flying bees (*Centris*, *Xylocopa*) visit these trees. But in the mass-flowering tropical shrub *Hybanthus*, although a variety of pollinating insects is attracted, only the little bee *Meliponia interupta* is important and cross-pollination is only ~10% (Augspurger, 1980). In Europe, blackthorn trees, *Prunus spinosa* (Rosaceae), produce masses of white flowers in spring before the leaves form, attracting a limited fauna of pollinators, including *Bombus* and the large, hairy syrphid fly *Criorrhina*. Orchard trees (apples, pears, cherries; also Rosaceae) are very showy too, and bees are very good at pollinating them. In fine weather 100 bees/ha can set an apple crop in 5 hours (van Emden and Service, 2004). *Bombus* spp. are effective pollinators of commercial raspberries. While these plants can self-fertilize, cross-pollinated flowers produce superior fruits (Willmer *et al*., 1994).

In alpine meadows, several flowers are blue or violet (attractive to *Bombus*), large and apparent, perhaps in some way to coax pollinators from lower altitudes, maybe by reducing the transit time between blooms. *Bombus* (Bingham and Orthner,

1998) and the fat and hairy-bodied butterfly *Parnassius apollo*, are important too (Kevan and Baker, 1983). Competition between plants for scarce pollinators and their ability to attract them from afar may be involved, while the stigmata are receptive for long periods. But pollination at low temperatures by warm-blooded insects bears a high energetic cost, which must be offset by greater fuel rewards from the plants (Price, P.W., 1997). Note here that laden bees fly back *downhill*. In Colorado, *B. appositus* are rarely short of nectar, but the harsh, sub-alpine weather restricts foraging time (Elliott, 2009).

On the other hand, it is thought that bees in physically favourable situations often compete for nectar (Michener, 1974; Michener, personal communication, 1985), indeed *Apis* may defend rich foraging areas close to their hives. An original alternative (Lovell, 1914) is that bee species are specialized to maximize their rate of uptake of both nectar and pollen, an early statement of *optimal foraging* (Section **10.2.3.9**). But these ideas are not mutually exclusive. Individuals that avoid flowers used more efficiently by other species (avoidance of competition) may maximize the collection of their products by specializing on different plants. Also foraging efficiency in *individual Apis* improves with practice (Ribbands, 1949). Indeed, learning is important in hymenopteran behaviour (Papaj and Lewis, 1993; Gumbert, 2000). The mud wasp *Sceliphron* constructs its first three cells progressively faster (Freeman and Johnston, 1978a), while several parasitic wasps employ associative learning (Section **8.2.2.1**). Foraging patterns of *Apis* are quite flexible (Wells and Wells, 1984). But in temperate situations, *Bombus* have the edge over other collectors of nectar because their advanced endothermic physiology allows them to forage both earlier in the year and earlier in the day (Heinrich, 1981). With the recent depredations of colony collapse disorder and the parasitic mites *Varroa destructor*, *V. jacobsoni* and *Acarapis woodi* on honeybees, *Bombus* species are in the front line as natural pollinators. Major pollinators among solitary bees include *Andrena*, *Anthophora*, *Centris*, *Megachile*, *Osmia* and *Xylocopa* (Klein *et al*., 2007). In developing conservation biological control (Section **13.2.4.7**), their enhancement (Mallinger and Gratton, 2015) and also that of *Eristalis* spp. should be considered (Rader *et al*., 2009). These and other hover flies are efficient pollinators of oilseed rape (Jauker and Wolters, 2008). On a rather sinister note, however, *Bombus* spp. can transmit Pepino Mosaic Virus to greenhouse tomatoes, either via pollen or damaged flowers (Shipp *et al*., 2008). These bees could also transmit Tobacco Mosaic Virus (Okada *et al*., 2000, in Shipp *et al*., 2008). The possibility that other insectan pollinators may spread viruses should be kept in mind.

Plants such as *Delphinium*, *Lythrum* and *Mentha* have floral spikes or similar vertical structures in which the lower flowers open first. Male organs develop first, then female ones, so avoiding self-pollination in the spike. In such genera, bees arriving and often bearing pollen from conspecific plants visit the lower flowers first, thereby transferring it to the receptive female parts. They ascend until they are in the male-ready zone, picking up pollen until they come to immature flowers, and then either go to another spike or fly off. The system may be co-evolved, bees pick up nectar or pollen and plants become cross-pollinated. But if the plant has several such spikes, the bee may transfer either 'self' or foreign pollen to them. So plants are in a dilemma of their own aims and the conflicting ones of pollinators (Price and Waser, 1979; Klinkhamer and de Jong, 1993). When pollinators visit an inflorescence they deposit some pollen on other flowers instead of exporting it all to conspecific plants. So the male part of plant fitness is compromised. Of course, in most species fertilization is massively inefficient for males. But it is also inefficient for pollinators to waste pollen that they use time and energy to collect. Thus, many bees have evolved specialized pollen collecting and retaining organs (corbiculae).

Female parts of the flower usually defend themselves by self-incompatibility (SI) mechanisms that prevent self-fertilization (Fisher, 1930; Brewbaker, 1957). SI is the inability of a plant producing functional male and female gametes to set seed when self-pollinated. There are heteromorphic and homomorphic SI systems. In the former, differences in the way that the stamens and styles are arranged identify the SI groups, as in pin and thrum flowers of primroses described by Charles Darwin. In homomorphic systems, all flowers being similar, are common. Only pollen from conspecific plants that is genetically different from that of the focal individual grows pollen tubes and effects fertilization. The system involves multiple alleles at a single locus and operates via pollen and stylar antigens (Li and Newbigin, 2002). SI pollen tubes grow slowly and fail to reach the ovules. This is part of a *pollen-selection system* that also excludes heterospecific pollen (Swanson *et al*., 2004). Cross-pollination is furthered when social bees transfer pollen among themselves in the nest (Heinrich, 1975). Even so, many lines of self-pollinating plants have evolved. For more information, see Charlesworth (1985, 2000).

Comparable to sperm competition in animals (Section **8.2.2.3**(**a**)), there may be pollen competition in plants. In plant populations individuals are selected to fertilize other individuals with increasing efficiency (Trivers, 1985; Maad and Nilsson, 2004). In bisexual plants, fitness has two components: via the female (seed bearing) and via the male (seed fertilizing) lines. These components may not be tightly correlated (Stanton *et al*., 1986; Strauss, 1997). Seeds spread genes from both sexes, pollen only from males. Apart from this, DNA in mitochondria and chloroplasts (mtDNA and cpDNA, respectively) are female transmitted (except cpDNA in conifers) (Petit and Excoffier, 2009). Since pollen is in general more widely dispersed than are seeds, so are genes coming from males.

Flowers have attracting and restricting mechanisms. Floral colour and arrangement in the inflorescence are components of attraction, luring a probably co-evolved pollinator. Insects see a different light spectrum than humans (Hinton, 1973; Briscoe and Chittka, 2001). Their visual range is often from ultraviolet (UV) to orange, ~330–540 nm, a shift of ~100 nm in comparison to humans. Red is not usually seen but insects are usually sensitive to ultraviolet (UV), blue and green. Bright red flowers are rarely pollinated by insects but are pollinated by birds, although several butterflies have red sensitivity. Such flowers tend to be large, showy, unscented and tropical, like *Spathodea* and *Hibiscus*. But avian pollinators must be small, like sun birds and hummingbirds, and very small birds are unsuited to cold and are mainly tropical. So, in the main, are big red flowers. Poppies in cereal fields seem odd.

In 1882, Lubbock showed that insects respond to UV light. In 1923, Richtmyer (in Hinton, 1973) described the UV patterns of many flowers. Some flowers that absorb UV light uniformly may contrast with their UV-scattering backgrounds (Frohlich, 1976). The Compositae often have yellow flowers due to flavanol glucosides, a UV-absorbing pigment. Just as we see a combination of blue and yellow pigments as green, insects with their ability to see UV, may see, say, yellow and UV in combination. Different flowers that look similar and all yellow to us should look different from each other to insects. Indeed, there is evidence from neural anatomy and behavioural studies on flies and butterflies that insects do use their colour receptors in combination (Kelber, 2001). Papilionid and pierid butterflies have red receptors with which they distinguish green from yellow. Dark patches and UV absorption patches at the base of some flowers are used as *nectar guides* by pollinators. But genes coding for floral colour might affect other traits (pleiotropy) such as resistance to enemies, since the biochemical pathways leading to pigment production, especially flavonoids, also lead to those employed in the synthesis of secondary compounds (Fineblum and Rausher, 1997; Section **2.4.2**).

In temperate regions, many early flowers are yellow, blue ones coming out later, although yellows persist during summer. But there are many reddish-purple flowers, such as mallow, red clover and thistle, which are bee or butterfly pollinated (Kevan and Baker, 1983). *Bombus* has a preference for violet (~410 nm) (Gumbert, 2000; Schaefer and Ruxton, 2009), with a lesser peak at ~515 nm. These bees learn rapidly to associate colour with reward. Even so, some greenish-yellow flowers, for example, linden (*Tilia*), ackee (*Cupania*) and ivy (*Hedera*), attract many insects. White surfaces reflect the most light, and flowers pollinated at night are generally glossy white, although some are also pollinated by day. They are also strongly scented, for example coffee (*Coffea*, Rubiaceae), citrus (*Citrus*, Rutaceae) and night-flowering cacti such as *Hylocereus* and *Selenicereus*. Darwin's famous orchid has flowers 'like stars formed of snow-white wax' and attracts a specific hawk moth. Nocturnal pollination exemplifies the sequential nature of much insect behaviour (Section **10.2.4.1**): scent attracts insects from a distance and the shiny white flowers from close up. Even so, some nocturnal hawk moths (**Fig. 8.1**) such as *Hyles* and *Deilephila*, have excellent colour discrimination at low light intensities (Kelber *et al*., 2002). Probably they use this ability to select flowers. Indeed, moths are usually the most important pollinators at night, although some halictid bees and *Apis dorsata* are active at this time.

Good examples of evolved restricting mechanisms are seen in those highly scented, night-pollinated flowers with a long, white corolla tube (*Lilium longiflorum*, Liliaceae, *Stephanotis floribunda*, Asclepiadaceae). However, in honeysuckle (*Lonicera*), although flowers are white and scented, attracting long-tongued moths at night to nectaries deep within the corolla tube, the style and stamens project, facilitating pollination. Darwin and Wallace found the orchid *Angraecum sesquipedale* from Madagascar with nectaries so deep (~30 cm) in the flower that they could be reached by no known insect. Darwin (1862) predicted the existence of a pollinating hawk moth with a suitably long tongue to reach the nectar, but not until 1903 was this moth discovered and named *Xanthopan morgani praedicta* by Rothschild and Jordan (Kritsky, 1991).

Bumble bees effect pollination of honeysuckle during the day, avoiding red unopened flowers and yellow dying ones. Large *Bombus*, with their long tongues, imbibe the nectar. Such bees and many moths have the high searching capability (Section **10.2.4.1**) necessary for efficient pollen transfer between conspecific plants. The bees are generally consistent to a given species during foraging (Free, 1970), often alternating their pollen and nectar trips. The petals of many flowers senesce rapidly after fertilization (Woodson, 2002) and in lupins change colour, which later bees tend to avoid (Nuttman and Willmer, 2003). These post-fertilization changes are driven in many plant species by the production of the phytohormone ethylene. But fallen flowers of *Trabebuia* retain their colour, effectively increasing the sphere of attraction (Section **10.2.4.5**) of the tree. Indeed, the attractive volumes produced visually and by scent have different shapes. A visual lure is essentially *sub-spherical* whose attractiveness is a function of inflorescence size, the potential pollinator's distance and visual acuity. But scents are wafted away by the wind in a *quasi-linear*, diffusing plume that becomes weaker with distance from source. Dusenbery (1989) showed theoretically that the optimal search paths for such different 'active spaces' should be downwind for the former and crosswind for the latter (Section **10.2.4.5**).

An advanced pollination mechanism, in which sticky packets of pollen (*pollinia*) are produced, has evolved in the Orchidaceae and the Asclepiadaceae (milkweeds). These are subtly transferred to specific areas of a pollinating insect by male mechanisms in the flower of one plant and unloaded onto the female part of another. In the orchid *Platanthera,* pollinia stick to the tongue or eye of its moth pollinators, giving variable efficiency (Maad and Nilsson, 2004). Insects of only a given size and structure can effect pollination, ones presumed to have a high chance of reaching a subsequent plant. Indeed, ~65% of orchid species are thought to have specific pollinators (Cozzolino and Widmer, 2005). Also, the pollinator cannot use the pollen. Male euglossine bees, in particular, pollinate orchids (Dressler, 1982; Ackerman, 1983; Fig. 8.2). They collect fragrant compounds from these plants and from other sources, but orchids seem more dependent on the bees than vice versa (Ackerman, 1983). Female euglossine bees go to other flowers (*Bixa*, *Clusia, Oncoba, Psidium*) to collect pollen. *Euplusia surinamensis* visits up to 180 *Cassia* and *Solanum* flowers to collect a single load (Janzen, 1971) and so are effective pollinators.

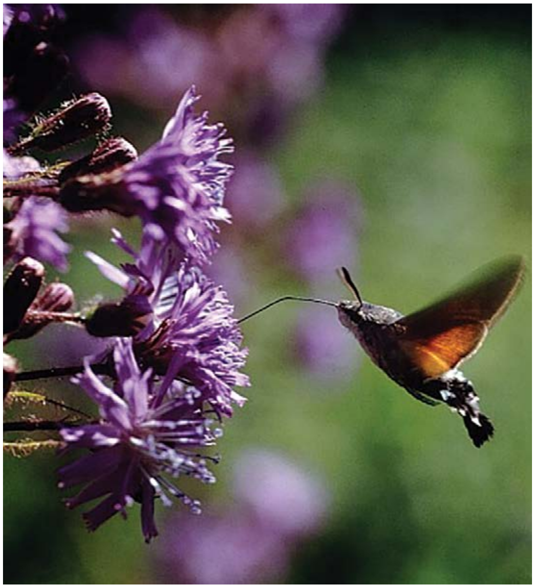


Fig. 8.1. Co-evolution example 1. Nocturnal pollination of *Cicerbita alpina* flower by the hummingbird hawk moth *Macroglossum stellatarum* (Sphingidae). Source: Wikimedia Commons, author Mg-K.

Fig. 8.2. Co-evolution example 2. *Euglossa bazinga* (Apidae, Euglossinae) about to pollinate a tubular flower. Source: Wikimedia Commons, author Eframgoldberg.

In these genera the tubular anthers extrude pollen only in response to vibration: such bees have a high wing-beat frequency. In the snapdragon (Scrophulariaceae) and gentians (Gentianaceae), pollinating bees have to be sufficiently big and strong to push into the floral interior. Occasionally, a further restriction is that the nectar contains toxins only a co-evolved pollinator can detoxify.

Bees (Greenleaf *et al*., 2007) and moths are major pollinators, but other insects, especially flies, play a role (Kevan and Baker, 1983; Buchmann and Nabhan, 1996). In Nematocera, mosquitoes pollinate *Habenaria* orchids, while ceratopogonid midges pollinate cocoa. In Brachycera, bombyliid flies (Section **8.2.2.5(e)**) often mimic bees and feed at flowers by hovering, *Bombylius discolor* having a proboscis >10 mm long. Calypterate Diptera (Larson *et al*., 2001) are key pollinators of Umbelliferae, which have flat inflorescences suitable for landing. In Compositae, syrphid flies in particular seek flowers of golden rod, *Solidago*. The figwort, *Scrophularia*, is wasp pollinated and numerous Parasitica need nectar for their energetic lifestyles (Gurr and Wratten, 1999). Chrysidid wasps (Section **8.2.2.5(x)**) often have elongated mouthparts, but their role as pollinators is poorly known.

Considered generally, three things make an effective pollinator: (i) its ability to pick up pollen from one plant; (ii) its ability to deposit it on a style of a conspecific plant at the right time; and (iii) the speed with which it does it. Bees, however, *are* essential for the successful pollination of several crops (Free, 1993). Top fruits such as apples, pears, plums and cherries (Rosaceae) all need bees for pollination and fruit set can be much improved by bringing in beehives. In China, solitary megachilid *Osmia* bees improve seed set and fruit size (Wei *et al*., 2002). *Megachile* spp. increase seed production in lucerne. Indeed, solitary bees, which comprise more than 85% of bee species, are important crop pollinators (Mallinger and Gratton, 2015). But red, white and alsike clovers all need either hive or bumble bees for proper seed set. In New Zealand, *Bombus* had to be established before red clover could be grown successfully. This crop is said to have as many as 500 million florets/ha, although an estimate for white clover in England (Freeman, 1967a) is a mere 64 million. *Bombus* spp. are used in many countries to pollinate greenhouse tomatoes. In Australia, the importation of such exotic bees is opposed on environmental grounds, but the indigenous anthophorid bee, *Amegilla chlorocyanea*, is an effective alternative. *Bombus terrestris* exists in New Zealand and is a good pollinator (Rader *et al*., 2009). In using insecticides on crops such as clover, there is often a conflict between killing pests, especially those attacking flowers, and protecting pollinators. Any spraying should be timed accurately to just before flowering and employ a short-term insecticide such as malathion (Freeman and Wimble, 1970).

Even though a flower is pollinated, its development into fruit and seeds is not assured. This may be arrested at an early stage because the pollen is incompatible, but also later because metabolic resources are limiting (Stephenson, 1981) or because the fruit is being damaged, often by an insect. When the period of flowering is long, abortion is more likely to happen to late flowers. Naturally, flower and fruit abortion has had consequences for insects attacking these structures (see **Chapter 6**), not only on mortality but also on dispersal.

8.2.1.2 Seed dispersal and protection

Although pollination is the best-recognized way in which insects assist plants (Bronstein, 1998), other co-evolutionary traits between them exist. While it is often hard to see if these traits are truly co-evolved or fortuitous, the latter provides a starting point from which true co-evolution might proceed (Janzen, 1980). Various associations between ants and plants are especially well developed in the tropics (Bronstein, 1998). In general, insects move pollen and birds and mammals move seeds (Section **8.2.1.1**). But there are several cases of seed dispersal by insects. Probably because teams of ants have been moving relatively massive objects to their nests for aeons, there are ~3000 recorded cases in which plants employ their services for seed moving (Gorb and Gorb, 2003). Species of *Camponotus* and *Crematogaster* carry seeds from Neotropical epiphytes in the Araceae, Bromeliaceae and Cactaceae to their arboreal nests, wherein these seeds germinate. Here chemical deception is probably involved, for the seeds contain methyl 6-methylsalicylate, which is also present in the ant's mandibular glands (Dettner and Liepert, 1994). As in entomophily, plants usually offer a reward for the insect's services. In these cases the seed coats are rich in lipids and fatty acids, and thus a *maternal structure* influences dispersal of the offspring (Starrfelt and Kokko, 2010). For the co-evolved system to work, as above, the ants must transport the seed to their nest to remove the nutritive coat instead of stripping it *in situ*, as in the plant genera *Croton* and *Trillium*. Carabid beetles also transport seeds (Manley, 1971), the North American *Synuchus impunctus*, for example, eats the caruncles of *Melampyrum*, discarding the remainder. Species of *Harpalus* and *Ophonus* also eat seeds (Zetto Brandmayr, 1990). Plants might produce seeds that biochemically mimic dead insects; after all, *Maculinea* larvae dupe ants into carrying them to their nest (Thomas *et al.*, 1998). Seed dispersal away from a perennial plant avoids parent/offspring competition (Motro, 1983; Starrfelt and Kokko, 2010), reduces their density and so may well lessen the chance of their being eaten. This is similar to the dispersal of larvae about to pupate from their food plant (Section **10.2.4.1**) and spreads risk in space (den Boer, 1968).

Associations between ants and plants are often mutualistic: both organisms provide protection for each other. Such an obligate association exists between some *Crematogaster* and *Pseudomyrmex* ants and swollen-thorn acacias in which they make their nests (Janzen, 1966; Fig. 8.3). The benefit of refugia provided by these trees with their large foliar nectaries is balanced by their enhanced growth rate in comparison to 'non-ant' acacias. Even so, the 'fly in the ointment' is the scarabaeid beetle *Pelidnota punctulata*, which is able to resist these aggressive ants, hence living at ease within their protective ambit. The Neotropical tree *Cecropia* attracts *Azteca* ants by producing glycogen, usually an animal polysaccharide, in Müllerian bodies. Under different light and nutrient conditions, they also produce attractive fat- and protein-rich 'pearl bodies' (Bronstein, 1998). Resident ants can reduce insect herbivory, and in *Cecropia* deter leaf-cutting ants (*Atta*) (Vasconcelos and Casimiro, 1997), that can defoliate a tree in a single night (Section **5.2.1.3(a)**). In Tanzania, ants such as *Crematogaster* live in pseudogalls on some *Acacia* trees, improving seed set (Willmer and Stone, 1997). Indeed, plant–ant mutualisms are very common. Ants can be rewarded from extra-floral nectaries (Holland *et al.*, 2009), distracting them from flowers, and hence pollination, and are cheaper to grow. These nectaries have also been implicated recently in inter-plant communication (Section **2.4.2**). For more information, see Huxley and Cutler (1991) and Bronstein (1998). Another mutualistic interaction is when plants attract the enemies of their insect herbivores, namely indirect protection (Wootton, 1994; Thaler, 2002; Section **2.4.2**).

Fig. 8.3. Co-evolution example 3. The swollen-thorn acacia *Vacachella drepanalubrum* and itsé inquiline, the ant *Crematogaster* sp. Source: Wikimedia Commons, author Pharaoh han.

8.2.2 Entomophagous insects

8.2.2.1 General introduction

A variety of insects eat other insects (*entomophagy*), and hence from our perspective may be beneficial. They are either: (i) *predators*, each individual whether male or female, juvenile or adult, *locating*, *attempting to kill, and eating* during its life several prey individuals (Vinson, 1984); or (ii) *parasitoids* (Reuter, 1913, in Godfray, 1994), in which only adult females oviposit in, on or near several hosts, the larval offspring attempting to consume and often finally killing their victim. Hence the term *parasit-oid*, as few true parasites kill their hosts. The generic term is 'enemy'. Predators may induce the dispersal of prey they fail to kill. Larval parasitoids, especially endoparasitoids, are frequently *killed by their hosts* (Sections **3.8** and **10.2**). Unfortunately, the erroneous idea that enemies always kill their victims persists (see Ives, 1991, and the cover of Godfray, 1994). While predators usually seek their prey on surfaces, aerial predators are common. As with bees (Section **8.2.1.1**), their area of operations is usually directly related to their size. Parasitoids largely seek their hosts by flight and so are more constrained by low temperatures than crawling predators. They usually come from the same taxonomic class as their hosts: the Insecta, very different from, say, helminth parasites of vertebrates (Bouletreau, 1986). While parasitoids mainly attack herbivores many exploit predatory and detritivorous insects and other parasitoids (*hyperparasitoids*). Their hosts are usually juvenile, more rarely adult insects or arachnids. Predatory insects search for, entrap or ambush their victims. Parasitoids search and rarely ambush (Vinson, 1984). Predators are high in the food chain, and so exist at relatively low population densities. While some forest moths have densities approaching 1 million/ha (Varley, 1949), several carabid beetles have ones in the range 1000–20,000/ha (Baars, 1979). Much lower densities are estimated for some common solitary wasps: 6–7/ha for *Cemonus lethifer* in the UK (Danks, 1971a), 30/ha for *Sceliphron* (Freeman, 1980) and 12/ha for *Zeta* (Taffe, 1983).

For both predators and parasitoids we re-enter the realm of co-evolution (Berry, 1985), this time + and –, so that we expect an *arms race*. Aggressors improve their attack, victims improve their *counter measures*. By stinging the host in specific parts of its nervous system, parasitic wasps often manipulate its behaviour to their own advantage (Libersat *et al*., 2009). Counter measures are: (i) primary ones operating at distance such as hiding, elimination of cues, like excising partly eaten leaves, crypsis and warning coloration; (ii) secondary ones operating once a victim has been contacted, such as armour, thrashing, dropping, or vomiting toxic fluid; and (iii) tertiary, internal defence by the host's immune system (Gross, 1993; Godfray, 1994), that is effective mainly against endoparasitoids (Section **8.2.2.5**). Therefore apart from movement, some parallels exist between the defence strategies of potential victims to those of plants against herbivores (Section **2.4.2**), for example, armour and toxins.

As above, prey may or may not escape predation and only rarely do they kill their predators. But the host's immune system often kills endoparasitoids (English-Loeb *et al*., 1990; Warren *et al*., 1992; Gross, 1993; Ohsaki and Sato, 1994; Strand and Pech, 1995), although occasionally both survive to adulthood (DeVries, 1984; Danyk *et al*., 2005a; Section **10.2.5.7**). It is increasingly understood that these systems are complex (Sullivan and Völkl, 1999; Schmid-Hempel, 2005; Gonzalez-Santoyo and Cordoba-Aguilar, 2012). But if a host does not kill its parasitoid it ultimately dies, rarely surviving to reproduce after the enemy has departed. Predators normally need prey as food for themselves, less commonly for their offspring (wasps, some ants). Facultative predators may also feed on dead insects, and in extreme cases such as earwigs, on plant material. On the other hand, some predators may kill far more than they consume, called *wasteful killing*, and this occurs more frequently at a high density of prey (Sunderland, 1988). Parasitoid females need hosts as food for the larvae, but often feed on them too (Howard, 1910; Jervis and Kidd, 1986; Kidd and Jervis, 1996; Heimpel and Collier, 1996) or otherwise kill them (Morris, 1965). Such behaviour is confined to species that lay yolk-filled eggs, and is rare in tachinid flies. In black scales attacked by *Metaphycus*, 75% of the scale's mortality is due to predation (de Bach, 1943), who records *Tetrastichus* killing 71% of asparagus beetle eggs by feeding. While feeding reduces the numbers of hosts, it does not increase directly those of the parasitoid (Section **11.5.2.3**). Also, sometimes parasitoids feed on *species* they do not parasitize. Such enemies are both parasitoids *and* predators. As with herbivorous insects, entomophagous insects pass energy between trophic levels. When predators consume part of their prey or when parasitoids feed as above, the leftovers are added to animal detritus (Section **8.2.4**). One of six things may happen when a foraging parasitoid attacks a host: (i) the host drives off the enemy; (ii) the female parasitoid feeds on and kills the host, so acting as a predator; (iii) the host is parasitized and the parasitoid's offspring emerge(s); (iv) the host is parasitized but kills the parasitoid's offspring; (v) both host and offspring survive; or (vi) much more often, both are killed by inimical environmental factors.

Predators and parasitoids in a community sometimes affect each other, not just herbivorous and detritivorous insects, adding further complexity to the energy flow in the ecosystem (Schoenly, 1990; Price, P.W., 1997; Rosenheim, 1998). Predators may eat parasitoids and parasitoids infest predators. Juvenile parasitoids, both conspecific and heterospecific, may kill each other (Freeman and Geoghagen, 1989; Ohsaki and Sato, 1994). The extent of such interactions and the ranges of victim species attacked are poorly known (Askew and Shaw, 1986). Generally, predators show scant intimacy but high lethality with their prey. Larval parasitoids show great intimacy and fairly high lethality with their hosts (Stiling, 1999). Predatory insects often attack a wider range of victims than parasitoids do, although sphecid wasps (Section **8.2.2.4(n)**) tend to be specific. In both groups cannibalism occurs and some predators (lacewings, ladybirds) may eat their own eggs. Finally, predators may reduce the visible effects of parasitoids when they kill and eat parasitized prey (Hawkins *et al*., 1997), as in point (vi) above. In Neotropical caterpillars, there is a complex indirect interaction between these two types of enemy (Gentry and Dyer, 2002). While the prey's defences, such as surface hairs, shelters and deterrent chemicals, are effective against predators, they may actually attract parasitoids. They suggest reasonably that victims well protected from predation provide *enemy-free space* (Simmonds, 1948; Atsatt, 1981) for parasitoids (Section **9.9**).

The means by which enemy insects find victims are influenced by whether they are residents or visitors. When resident, as assumed in many host/parasitoid models (Section **11.5.3.2**), only close-range cues are needed, especially visual, olfactory or tactile ones. But reality is complex. Recall that most parasitoids, unlike most predators, need to find foods such as nectar and honeydew and often leave the proximity of their hosts to refuel. Also recall that nectar contains amino acids (Section **8.2.1.1**). Parasitoids often move repeatedly though the hierarchy of habitat and patch to find resources (Vinson, 1976, 1984; van Alphen and Vet, 1986; Vet and Dicke, 1992; Section **12.2.1**), allocating appropriate time to each (Casas *et al*., 2003). Also, age may affect their behaviour. For example, young female *Pimpla ruficollis*, a parasitoid of pine shoot moths, *Rhyacionia buoliana,* are repelled by the odour of pine trees (pinene), but when >6 weeks old they are attracted by it (Thorpe and Caudle, 1938), a trait promoting initial dispersal, but later improving host location. Two other ichneumons afflicting this moth, *Coccophagus turionellae* and *Itoplectis conquisitor*, are also attracted to pine resin odour (Godfray, 1994), who defines three spatial levels of attractive signals: (i) those from plant patches used by potential hosts; (ii) those caused by the presence of hosts in such patches; and (iii) those from the hosts themselves. The aphidiine parasitoid *Diaeretiella rapae* finds its aphid victims on brassicas by being attracted to the allyl isothiocyanate these plants produce, but does not on non-crucifers (Price, 1992). The plant's volatiles, mediated by anemotaxis (Section **10.2.4.3**), determine the existence of the interaction. Bacteria associated with herbivores may also be a source of chemical information. But as usual, the reliability of information decreases with distance (Vet and Dicke, 1992).

Several Parasitica, such as the ichneumons *Exeristes roborator* and *I. conquisitor* (Wardle and Borden, 1985), the braconid wasps *Cotesia marginiventris* and *Microplitis rufiventris* (D'Alessandro *et al*., 2006), the chrysidid wasp *Argochrysis* (Rosenheim, 1987) and the tachinid fly *Drino bohemica* (**8.2.2.5(h)**), employ associative learning (Taylor, R.J., 1974; Vet and Dicke, 1992; Papaj and Lewis, 1993). They often associate visual and olfactory cues (Feener and Brown, 1997) with their host. Naïve females do not show this effect, but once they have parasitized a host associate olfactory cues with the event. *Microplitis croceipes* has a strong learnt preference for both visual and olfactory cues emanating from its host's micro-environment (Godfray, 1994).

The winter moth's tachinid parasitoids are attracted to chewed oak foliage. Feeding by the host larva causes the release of a special attractant, suggesting + + co-evolution between plant and parasitoid (Sections **8.2.1** and **8.2.2.5(k)**). But generally, it seems that the enemies of herbivores are attracted to plant odours first (patch location), then to damaged plant tissue and finally to the victim itself, moving progressively through finer levels of resource space (Section **12.2**) in the process (Salt, 1935; van Alphen and Vet, 1986). For example, *Glyptapanteles flavicoxis*, a braconid parasitoid of the gypsy moth, is attracted to undamaged poplar foliage, more so to that damaged by host larvae, but also to their frass (Havill and Raffa, 2000), much as Godfray suggests. In an early paper J.M. Smith (1957) found that two *Aphytis* parasitoids show distinct preferences for different food plants of red scale insects (Section **6.3.2.2(a)**). If parasitoids react to plant odours from some of their victim's food, but not to others, the latter provides *parasitoid free space* (Section **9.9**). For more examples of host finding, see Turlings *et al.* (1995) and Takabayashi and Dicke (1996). Parasitoids may need these cues in combination (Vinson, 1984) and react to the same chemicals used by their victims: ecomones from plants, sex pheromones and even mating calls (Zuk and Kolluru, 1998). For example, calling crickets *Gryllus* and *Teleogryllus* attract the tachinid flies *Euphasiopteryx* spp., while several long-horned grasshoppers similarly attract *Ormia*, *Therobia* and *Homotrixa*.

Parasitoids often play a major role in the natural control of insect numbers, but perhaps not so often as thought formerly (Section **10.2.3.9**). For insects such as leaf miners and gall midges, they often kill >50% of the juveniles (Freeman and Geoghagen, 1989; Cornell and Hawkins, 1995; Gröbler and Lewis, 2008) and their population density may be linked to that of their host in a way that assists natural control (Hassell, 1998a, b; Section **11.5**). But in insects in the soil and bark beetles, parasitoids are less significant, although there can be many attacking species (Section **4.2.1.2(h)**). Predators, too, may play a significant role in prey mortality. For example, the larvae of lacewings, ladybirds and syrphine flies each consume several hundred aphids or other small bugs during development.

Of course, both predators and parasitoids are employed extensively in biological control (= biocontrol), and we shall note many specific examples. Despite some older arguments to the contrary, Hall and Ehler (1979) estimated that both groups have similar success rates. Biocontrol has been used when a herbivorous pest species comes into a new region, often a new continent, for the first time (Section **13.2.4.6**). Lacking specialist natural enemies it may increase at an alarming rate, a rate that gives one some idea of the impact that these insects can have in population limitation. A search for such enemies in the pest's place of origin has led to their identification and culture. Their release resulted in complete control in ~16%, and a great reduction of the pest's population in ~58%, of cases attempted (Pedigo, 1996). This strategy, termed *classical biological control*, is comparatively cheap, invasive, often self-perpetuating and fairly friendly to the environment (Howarth, 1991) – it should always be investigated (Luck *et al*., 1988). But in the remaining ~26%, often because of rather different physical conditions, the method has failed. To compare these conditions one can use hygrothermographs (Section **10.1.1**) from both regions, and enemy biotypes that best match the new environment can be tried. However, the problem of cryptic species among the imported parasitoids can lead to confusion (Walter, 2003), while the presence of undetected hyperparasitoids (Section **8.2.2.5**) may or may not interfere with their action (Rosenheim, 1998). A further consideration is that inbreeding in culture may affect the sex ratio (Waage, 1982; Godfray, 1994) and other attributes of these potential agents (Bigler, 1989).

We consider here the important groups of entomophagous insects, not exhaustively, since such information may be obtained from the standard texts. But it provides a handy compendium, a '*who's who*' of the groups engaging in this behaviour and gives an idea of their diversity and complexity. Some standard works on entomophagous insects are Clausen (1940, 1978), Askew (1971), de Bach (1974), Huffaker and Messenger (1976), Price (1980), van den Bosch *et al*. (1982), Waage and Greathead (1986), de Bach and Rosen (1991), Godfray (1994), van Driesche and Bellows (1996) and Quicke (1997).

8.2.2.2 Predators

Insects face great mortal risk from predatory insects in most environments. These assassins operate: (i) on and in the soil (cicindelid, carabid, histerid and staphylinid beetles); (ii) on foliage (mantids, lacewing larvae, reduviid, anthocorid and mirid bugs, coccinellid and some carabid beetles, dolichopodid flies, syrphine larvae, ants); (iii) in the air (dragonflies and asilid flies); (iv) in water (odonate and stonefly nymphs, specialized Heteroptera and dytiscid beetles); and (v) in carrion (cyclorrhaphan flies and staphylinid beetles).

Predators may have advantages over parasitoids as biocontrol agents as they are nearly all polyphagous, alternative prey usually sustaining their numbers when the focal pest is at low density. Nor do they often require nectar sources to sustain activity, as parasitoids often do. Although the host range of few parasitoids is well known (Askew and Shaw, 1986; Vet and Dicke, 2011), only a few are quite restricted (*oligophagous*), while many have a wide host range (*polyphagous*) (Thompson, 1943; Bushing, 1965; Shaw, 1994; Salvo and Valladares, 1997). Oligophagous predators, however, are often better for biocontrol because, while having alternative prey, they respond faster to changes in the densities of their target victim. Then, both sexes of predators eat prey while only female parasitoids affect their victims directly (Section **8.2.2.1**). And predators can kill their prey instantly whereas koinobiontic parasitoids take some time to do so (Section **8.2.2.5**), a period in which the host may still be damaging a crop. Many female parasitoids, however, feed on and kill the host species (Flanders, 1953; Jervis and Kidd, 1986). Apart from these differences, generalized enemies use generalized cues, while specialized ones use specific cues to find their victims. Also, crawling predators usually operate at lower temperatures than flying parasitoids do. Aquatic predators, either above or below the water surface, may reduce the numbers of medically significant Diptera, especially those in the Culicidae and Simuliidae.

But the numbers of predatory insects may not respond fast enough to control the increasing density of their prey (Section **11.2.2.5**). Effective ones should, therefore, be voracious both as adults and larvae, have a long adult life, a high fecundity and rapid development. Such features are found in many ladybirds (Section **8.2.2.4**(e)), a family epitomizing the ideal predatory insect (Fig. 8.4). These considerations aside, tolerance to insecticides by all natural enemies is a distinct advantage for any candidate for biocontrol, and indeed has been acquired by a few of them. We will deal with these beneficial insects in taxonomic order.

8.2.2.3 Exopterygote predators

Because development in these insects is gradual, we expect nymphs and adults to share similar predatory lifestyles. While this is so for orthopteroids and hemipteroids, which are the majority, the aquatic juveniles of palaeopteroids do not share the environment of their terrestrial adults.

8.2.2.3(a) ODONATA; ANISOPTERA AND ZYGOPTERA. Dragonflies; damselflies, 5500 spp. This palaeopteroid group has great antiquity, dating from the Upper Carboniferous, when huge proto-dragonflies, such as *Meganeura* with up to a 70 cm wingspan, hawked the Earth. *Namurotypus*, dating 325 Ma, had longer antennae and a less modified thorax than modern species. The Norse regarded dragonflies as heralds of the goddess Frigga, wife of Odin, which is why with the spread of Christianity they became associated with the Devil, for example, in the popular name 'Devil's needles'. Today, we should regard them, more sensibly, as sophisticated predatory insects with a long evolutionary history, perhaps as aerial sharks (Fig. 8.5). Alone among exopterygote insects they have evolved a flight capability comparable to the higher Diptera and Hymenoptera. They possess huge eyes, *Anax junius* having >28,000 ommatidia in each one, and the greatest visual acuity of *any* insect (Land, 1997). Compared to locusts, another group of exopterygotes, their visual systems permit a much more sophisticated level of control (Section **10.2.4.1**; Taylor and Krapp, 2008). They use patterns of polarized light to detect water, then, each eye has a specialized band giving high resolution for tracking prey, which they catch and retain in their bristly legs. These are set forward with their bases only a little behind the head and form a raptorial basket, making them unsuitable for much walking. But while the leg muscles also function in the flight mechanism of most insects, they are independent of it in dragonflies. These unique predators show the evolutionary perfection of four-winged flight (Brodsky, 1994). The bi-motor mechanism, with the hindwings about a quarter out of phase with the forewings (you can see this when they hover), allows great manoeuvrability. Some dragonflies pursuing prey can even somersault to reverse direction.

Dragonflies commonly eat Diptera: tsetse in Africa and calliphorid flies everywhere, but while they are opportunistic predators, >80% of their prey are flies (Corbet, 1999). They are often seen capturing insects disturbed by harvesting, following the big machines like gulls behind a plough! Overall their hunting strategy is of two types: (i) *hawkers* use air to air attack; and (ii) *perchers* or *darters* normally use ground to air attack, in essence a 'sit-and-wait' strategy. A similar division exists in the mate-finding

Fig. 8.4. The beetle *Rodolia cardinalis* (Coccinellidae) devouring the scale insect *Icerya purchasi* (Margarodidae), a first major success in biological control.

Fig. 8.5. An aeshnid dragonfly (Odonata): an aerial shark. Fore- and hindwings beat out of phase. While primitive in origin these predators are among the most sophisticated flying insects. The legs are tucked in tightly, so reducing drag. Source: Wikimedia Commons, author Tony Hisgett.

behaviour of some male butterflies (Berwaerts *et al.*, 2002). Dragonflies of the two behavioural types have appropriately different eye structure (Land, 1997) and wing loading. While hawkers are largely endothermic, perchers are largely ectothermic (May, 1979; Section **10.2.4.2**). But all dragonflies, like tsetse, need several days to attain full flight capability (Marden *et al.*, 1998; Marden, 2000). The numbers of mitochondria in microscopic sections of wing muscle trebles during this period and flight activity is greatly increased. Hawkers (Aeshnidae) have a large wing area relative to total body mass (low wing loading) and a thoracic mass <45% of the total. They conserve energy by gliding and use thermals like avian raptors. Adults spend much time planing over the feeding area (*Pantala*, *Tramea*), patrolling a territory (*Aeshna*, *Anax*) or foraging along streams (*Cordulegaster*). Of course, they are numerous along rivers. The pantropical *P. flavescens* catches mosquitoes over paddy fields in Cambodia and over cricket fields in Jamaica. This species and *T. basilaris* are recorded hill-topping (Section **10.2.4.1**) in South Africa. Groups of these dragonflies can be seen hunting in the lee of windbreaks such as hedges, where small flying insects gather (Trevor Lewis, personal communication). A hunting phase often occurs before reproduction and may include migration (Corbet, 1999). Feeding areas may be far, indeed kilometres, away from aquatic areas where they breed. *Libellula quadrimaculata* migrate *en masse*, while Glick (1939) caught an *Anax* species at >2000 m. In other genera hunting for food always occurs close to water bodies.

The darters (Libellulidae), such as *Libellula, Sympetrum* and *Somatochlora*, attack their prey from a perch near water where they bask to elevate their body temperature (T_b; Heinrich, 1993), the broad abdomen functioning to pick up insolation. They have a high power to mass ratio, the muscular thorax sometimes being >65% of the total body mass (Marden, 2000). Some *Libellula* can accelerate equal to 2.5 g and they have great manoeuvrability, during which they may generate even higher g-forces. But this group may also hunt on the wing and *Pachydiplax* is recorded repeatedly passing through swarming Diptera. The number of perching sites, acting as resources (Section **9.8**), affects the local density of male *L. fulva* and also the frequency of aggression between them (Macagno *et al.*, 2008), who report different patterns of movement between the sexes in this species. Fishes may eat ovipositing females and bee-eaters catch both sexes.

Odonate copulation involves a strange conjunction of the appropriate parts. The male organs involve the second and third abdominal sternites, into which a receptive female inserts her terminal genitalia. Pairs often remain *in copula* for periods longer than required for sperm transfer. As in locusts and dung flies males extend this period so preventing other males mating with the same female and thereby supplanting their sperm, a feature, '*sperm competition*', common in animal reproduction (Trivers, 1985). Odonate nymphs are predators in water bodies and so, as we noted, may reduce the numbers of aquatic Nematocera whose adults transmit several lethal or debilitating diseases (Section **7.1.1.2**). They are also commonly cannibals, as in *Lestes*, the larger consuming the smaller (Corbet, 1999), a mechanism self-limiting their population size. While there is no true pupal stage in exopterygotes like these, the transformation from an aquatic to an aerial predator is extreme.

The damselflies are generally smaller, slower-flying relatives of dragonflies, but despite their frail appearance can be migratory. Naturally, they prey on smaller insects like midges and mosquitoes and are sometimes eaten by their more robust relatives. Species of the Calopterygidae sport metallic coloration of their bodies, bright wings and sexual colour dimorphism. The Lestidae are also often metallic, the nymphs living in still/stagnant waters. The Neotropical genus *Megaloprepus* preys on orb-web spiders (Fincke, 1992).

8.2.2.3(b) MANTODEA. 1800 species. Preying mantids are orthopteroids related to cockroaches: they deposit eggs in a similar *ootheca* to theirs, but are voracious predators. They employ cryptic coloration and a sit-and-wait strategy (Fig. 8.6), but they may also stalk prey. Like odonate nymphs, they are cannibals. Mantids are largely tropical or Mediterranean and some big Neotropical ones are >10 cm in length. They even attack tree frogs, small birds and insectivorous mammals. More usually they prey on tettigoniid grasshoppers, katydids, flies and caterpillars. In the Dermaptera, *Forficula* (Section **6.2.1.1(a)**) eat aphids and insect eggs, being effective predators in apple orchards.

8.2.2.3(c) HETEROPTERA; Reduviidae and related families. Reduviid bugs are a well-developed group of predators in the Neotropics, attacking insects as well as mammals (Section **7.3.1.1**; see Fig. 9.5(a)). They often have a narrow head with prominent

Fig. 8.6. The mantis, *Mantis religiosa* (Mantodea), a sit-and-wait predator on foliage. Source: Wikimedia Commons, photographer Christian Ferrer.

eyes, and a long, curved proboscis. Many are brightly coloured. They capture prey either with powerful front legs that as in *Metapterus* are raptorial, or these legs form sticky brushes to which hapless victims adhere. *Arilus cristatus*, the large, black 'wheel bug' of North American orchard trees, preys on caterpillars, while *Zelus renardii* is known popularly as the 'leafhopper assassin'. Males in this genus guard the egg batch they have fertilized. *Peregrinator biannulipes* may be found feeding on stored product pests. In India, *Harpactor costalis* preys on another bug *Dystercus cingulatus*, which it resembles, a device known as *aggressive mimicry* (Section **10.2.3.5**). In Australia, *Pristhesancus plagipennis* has been used in trials to control *Heliothis* and *Creontiades* on cotton (Section **13.3.2.3**).

The Phymatidae are rather similar to the Reduviidae and have prominent eyes. Some are cryptic, sit-and-wait predators of bees and flies visiting flowers, a habit like that of thomisid spiders, a few mantids and the Nabididae. Nabid bugs feed on small insects like aphids. While most phymatid bugs are tropical, a few species of *Phymata*, such as the large *P. erosa*, are found in North America. Some *Nabis* spp. are interesting in having raptorial fore legs and eating the larvae of predatory *Chrysoperla* (Neuroptera; Section **8.2.2.4(a)**). They may also show alary polymorphism. *Nabis capsiformis* is a beneficial pantropical predator found on many crops, *N. ferus* is a numerous Palaearctic species, while *N. americoferus* is North American and a predator of aphids.

The Anthocoridae also contains many predators, having a high rate of increase and good searching ability. They are mainly small, black and white, and often live on foliage and flowers, but have been trapped at heights of 1000 m in work on aerial migration. Many species eat insect eggs, aphids, other small bugs, small insects in general and even mites. *Anthocoris nemorum*, *A. confusus* and *Orius vicinius* are common in Europe, while in North America *O. insidiosus* eats the larvae of the moths *Heliothis* and *Ostrinia*. *Orius albidipennis* and *O. insidiosus* are used to control thrips, and *Deraeocoris brevis* various homopteroids. *Orius tristicolor* eats whiteflies on cotton in Arizona, while *Xylocoris flavipes* attacks several stored-products beetles.

Predatory heteropteran bugs also exist in families that are largely phytophagous. For example, *Macrolophus caliginosus* is a predatory mirid bug used in the biocontrol of whiteflies. The Pentatomidae contain several predatory species including *Podisus maculiventris*, which attacks lepidopteran larvae, and *Zichrona caerulea*, which feeds, both as nymphs and adults, on flea beetles. The Belostomatidae, Naucoridae, Notonectidae, Nepidae, Gerrididae and Veliidae, comprise aquatic predators (Richards and Davies, 1988).

8.2.2.4 *Endopterygote predators*

Unlike exopterygotes (Section **8.2.2.3**), we do not expect carnivory necessarily to occur in conspecific juveniles and adults. None the less, both adults and larvae *are* often predatory, as in carabid, dytiscid and coccinellid beetles, and in lacewings. In social and solitary wasps the adult females feed the larvae mainly insect food. But there are many cases where the larvae but not the adults are predatory, as in syrphine flies and in the moths *Eupithecia*.

8.2.2.4(a) NEUROPTERA. 6000 species. This primitive, endopterygote order contains several families of predatory insects. Most curious are the Mantispidae. They are largely tropical and look like delicate preying mantids, but they have characteristic net-veined, neuropterous wings arched over the back (Fig. 8.7). Brown and the green lacewings, Hemerobiidae and Chrysopidae, respectively, are common worldwide. The eggs are sessile in the former but have long pedicels in the latter, reducing enemy attack and cannibalism (Danks, 2002). Their larvae are insatiably predaceous, particularly on aphids and other small homopteroids. The

Fig. 8.7. The mantispid, *Climaciella brunnea,* parallel evolution with mantids. Source: Wikimedia Commons, author Judy Gallagher.

green lacewing *Chrysoperla carnea*, which is migratory, has been used in biocontrol. Its larvae eat many cereal aphids during the sensitive flowering period (Section **13.3.2.2**). Two sibling species exist: *C. carnea* is generally distributed while *C. downsei* prefers dense forest. The adults of some species will open leaf mines and consume the larvae, just as some predatory ants do. Additionally, *Chrysopa* has aphid-eating adults (Albuquerque *et al*., 1997). The larvae in some genera, such as *Mallada* and *Suarius*, carry debris on their backs, presumably for concealment. The Myrmeleonidae have larvae called ant lions. These excavate small, conical pits in dry soil and consume the insects, commonly ants, which fall in. While this is a remarkable sit-and-wait strategy, these creatures are of little importance to the economic entomologist. *Myrmeleon* is widely distributed. The adults are delicate and superficially resemble damselflies, but they have clubbed antennae and a different flight pattern.

The Mecoptera comprise a small order with predatory or scavenging larvae in the soil. The aerial adults often favour damp woodlands but have similar habits to the larvae. The two major genera are *Panorpa* and *Bittacus*.

8.2.2.4(b) COLEOPTERA; ADEPHAGA; Cicindelidae, Carabidae. Tiger beetles, ground beetles. These are ancient, massive groups (30,000 species in total) with fossil forms dating from the Jurassic. Both larvae and adults are major predators of terrestrial insects, 'adephaga' being derived from the Greek for 'voracious', although this rather overstates the case. Their prey are subdued rapidly by the injection of digestive enzymes from the midgut. Many feed on the ground; the fast-moving cicindelid genera *Cicindella*, *Manticora, Omus* and *Platychile* hunt by day, while most carabid beetles, especially the larger ones, hunt by night (Luff, 1978). They rarely damage plants, but a few ground beetles consume seeds (Manley, 1971; Frank *et al*., 2010), attack strawberry fruits (Alford, 2007) or eat winter wheat (*Zabrus tenebrioides*). Many carabid adults cross open ground in the daytime, especially when moving from winter to summer habitats. Hinton (1973) found that their elytra possess diffraction gratings, producing warning coloration in sunlight, deterring predators at such vulnerable times, and making it hard for a predator to judge distance. But they remain cryptic black in shade.

Collyris and *Tricondyla* (Cicindelidae) and some Carabidae eat insects on plants. *Demetrias atricapillus* and *Poecilus cupreus* eat cereal aphids, the latter often reducing and delaying their peak densities on winter wheat (Winder *et al*., 2005). *Calosoma* eats caterpillars, *C. sycophanta* having been used in attempts to control gypsy moths (Section **5.2.1.4(f)**). The abundant *Harpalus rufipes* attacks cereal aphids and *Pieris* larvae. Other carabid genera eating insects on plants are *Agonum*, *Feronia* and *Trechus*. In the USA, *Lebia grandis* often eats Colorado beetles, but its larvae *parasitize* the pupae. Larval bombardier beetles (*Brachinus*) parasitize the pupae of some water beetles (Juliano, 1986). In all, the larvae of some 500 carabid species are parasitoids.

Tiger beetle larvae usually live in vertical burrows in the soil and behave as sit-and-wait predators at the entrance, dragging prey down to consume it. In severe drought they may seal the burrow and become quiescent. They often take a year or more to develop (Pearson and Knisley, 1985). In an interesting study in Borneo, Rees (1986) found that adults of both these families possessed a very heavy skeleton (~25% of wet body mass), relatively much heavier than that of chrysomelid beetles (~11%), for example. Where prey are captured infrequently, nitrogen to build the skeleton (both protein and chitin contain nitrogen) may be short and is a reason for their slow growth (see White, 1993). Their parasitoids include *Anthrax* spp. (Bombyliidae) that deposit eggs in the burrows, often while still in flight, thus avoiding being eaten. *Spogostylum anale* is another bombyliid parasitoid in North America (Shelford, 1913), where five *Methocha* spp. (Tiphiidae) are also parasitoids, and may seal the beetle's burrow after their attack. Adult tiger beetles have large eyes, long legs and are unusually active, running rapidly (0.5 m/s) and taking flight readily. *Cicindella* adults maintain T_b at around 35°C by a variety of behaviours, basking when too cool and burrowing and walking on ‘tip toe’ (‘stilting’) when too hot (Dreisig, 1980, in Willmer, 1982), while the bright, metallic colours of many species serve to reduce heating (Section **10.2.4.2**). Despite their aggressive name, they are eaten in the air by asilid flies, and on the ground by birds and lizards. Apart from their agility and often warning coloration, they defend themselves with volatiles such as benzaldehyde and benzoyl cyanide secreted from pygidial glands (Pearson, 1985). In temperate regions, the adults dig burrows in autumn and hibernate.

Ground beetles comprise much the larger family being one of the largest in the order. Genera with long legs (*Carabus*, *Harpalus*) are runners, those with short legs (*Clivina*) are diggers. Several species, including Harpalus rufipes and the nocturnal *Agonum dorsale*, consume dislodged aphids on the ground before they can creep back to the crop. *Trechus quadristriatus* eats eggs of carrot root flies and other Diptera on the ground. *Scaphinotus* devours snails. Not all carabid beetles fly and some genera even have fused elytra. Other genera (*Agonum*, *Pterostichus*) are wing dimorphic. Those that hibernate as adults often migrate in spring, while those that pass the winter as larvae normally fly in summer. *Notiophilus biguttatus* flies as a mass migrant. In some species of *Agonum*, *Calathus* and *Pterostichus* adults can reproduce in two consecutive years, and *Brachinus* reproduces only after its first year of adult life (Juliano, 1986). In the UK, *Phaenoserphus viator* and *P. pallipes* (Proctotrupidae) parasitize some carabid larvae (Critchley, 1973), and *Microctonus* spp. (Braconidae) affect some adults (Luff, 1976). For *Calathus* and *Pterostichus* on a Dutch heath, pathogenic nematodes cause high egg mortality, while larval death results from their limited ability to locate food (van Dijk and den Boer, 1992). The physical conditions in the soil, especially temperature and moisture, are critical, but density dependence (Section **10.2.3.7**) is unimportant. For more on these fascinating beetles see Thiele (1977), Luff (1978, 1982), den Boer *et al.* (1986), Pearson (1988), Stork (1990), Lövei and Sunderland (1996) and Holland (2002). The taxonomy of British Carabidae has been revised by Luff (2007), the book having beautiful illustrations.

All stages of dytiscid and gyrinid beetles, which are also in the Adephaga, are aquatic predators, although the adults are capable of long flights. *Dytiscus* spp. are large, may live up to 5 years, and attack a wide range of other aquatic insects, worms and even small fishes. As in *Brachinus*, their long reproductive life suggests that they have low adult mortality rates. Some gyrinid beetles form spinning, mating aggregations on the surface of ponds and are dubbed ‘whirly-gig’ beetles.

8.2.2.4(c) COLEOPTERA; POLYPHAGA; Histeridae.

>3000 species. These beetles are active predators both as adults and larvae, commonly on other beetles but also on a variety of small arthropods. *Carcinops pumilio* (temperate) and *C. troglodytes* (tropical) inhabit stores where they eat stored-products pests. *Teretriosoma nigrescens* is a specific predator of *Prostephanus truncatus*, a Central American bostrychid beetle that attacks stored maize. *Saprinus* eats grasshopper egg pods while *Hister pustulosus* and *H. sextriatus* attack cutworms and other noctuid larvae. Other species eat maggots in carcasses.

8.2.2.4(d) COLEOPTERA; POLYPHAGA; Staphylinidae.

Rove beetles; >30,000 species. Rove beetles are elongated but have short elytra. This allows body flexibility in relation to their habit of searching for prey in loose soil, leaf litter, decaying wood and carrion. Some species, however, feed on detritus and/or fungi. Despite their abbreviated elytra, the metathoracic wings are often long, folded in a complex manner, and used in rapid take off and effective flight (Richards and Davies, 1988). Rove beetles may also seek ant and termite nests. Great variation exists in body size, and of course prey size varies accordingly (Fig. 8.8). Different staphylinid species live in wet or dry soils. For example, *Stenus incrassatus* favours very soggy conditions, *Staphylinus erythropterus* dry soil, but *Stenus geniculatus* a wide range of soils. *Tachyporus* spp. climb cereal stems and devour aphids. Other species are major predators of young carrot and cabbage root fly larvae (Sections **3.2.2.1(h)** and **3.2.2.1(i)**), and other soft-bodied pests in the soil. Unlike many carabid beetles they may fly into fields from afar. But like them, >500 staphylinid species are parasitic. Larval *Aleochara* develop in the puparia of cyclorrhaphan Diptera. They are prone to employ chemical deception. Adult *A. curtulabut* consume blow fly maggots on carcasses, where mature males are mutually aggressive. Young and weak males, however, produce female sex pheromones, the deception thwarting such attacks (Peschke, 1990, in Dettner

Fig. 8.8. The ground-dwelling Devil's coach horse beetle *Ocypus olens* (Staphylinidae). Insects washed off plants by rain are often eaten by such predators. Source: Wikimedia Commons, © Entomart.

and Liepert, 1994). The predatory larvae of *Atemeles* and *Lomechusa* use chemical deception in the brood chambers of *Formica* ants. Finally, the Neotropical *Leistotrophus versicolor* traps drosophilid and phorid flies, which often lay eggs on dung, by depositing a malodorous secretion on the forest floor.

8.2.2.4(e) COLEOPTERA; POLYPHAGA; Coccinellidae. Ladybirds. Some other predatory Polyphaga. Familiar ladybirds are one of the most beneficial predatory groups and one of the best studied (Hodek *et al*., 2012), at least in the laboratory. They feed on injurious pests (aphids, psyllids and scale insects) and have been used in several successful cases of biocontrol. From as early as the 1930s, the US mail order company Sears sold these robust little beasts directly to farmers. Several species are effective predators of cereal aphids in North America, including *Hippodamia convergens*, *Scymnus frontalis*, *Coccinella septempunctata* and *Coleomegilla maculata*. In Europe, *Adalia bipunctata*, *Coc. septempunctata* and *Propylea quatuordecimpunctata* are found in cereal crops. The most famous and earliest use of biocontrol is of *Icerya purchasi* on Californian citrus by *Rodolia cardinalis* from Australia (see Fig. 8.4; Section **13.2.4.6**). In Australia, *Coc. trifasciata* reduces numbers of *Acyrthosiphon pisum*. Another Australian species, *Cryptolaemus montrouzieri*, is mainly herbivorous but often feeds on *Heliothis* in cotton bolls (Section **6.2.1.2(d)**). Other biocontrol agents on small homopteroids are *Ad. bipunctata*, which has been successful in Switzerland in reducing *Dysaphis* on apple, and *Cybocephalus nipponicus, Delphastus pusillus* and *Harmonia axyridis*. *Stethorus punctillum* eat mites. *Epilachna* is a leaf-feeding genus that, like several chrysomelid beetles, can transmit plant viruses (Fulton *et al*., 1987).

Although most ladybirds are univoltine, their success in biocontrol is undoubtedly due to their high rate of population growth (Section **13.5.2.1**) and extreme voracity of both the larvae and adults. A *Hip. convergens* larva can consume daily its own mass in prey and up to 50 aphids as an adult. Across coccinellid species, however, food quality has inconsistent effects on reproductive success (RS). In culture, *Coc. septempunctata* larvae use honeydew from *Sitobion avenae* as an arrestant and as a searching stimulant, while *Hip. convergens* adults are attracted to the alarm pheromone of their prey (Carter and Dixon, 1984). Mating is frequent with both sexes being promiscuous, and involves the transfer of a spermatophore (Nedvěd and Honěk, 2012). In *Ad. bipunctata*, polyandry increases AF and hatching rate. AF is fairly high, averaging ~140 in this species in the UK. *Coccinella novemnotata* in the USA lays ~600 eggs in the field, but >1500 over a 3-month period in the laboratory (Shannag and Obeidat, 2008). Cannibalism of the eggs by larvae hatching early occurs in several species (Polis, 1981; Mills, 1982; Martini *et al*., 2009). Development takes only 4–6 weeks for several species. The *larvae* lay down an oviposition deterring pheromone (Section **10.2.4.7**) that limits further oviposition in their vicinity. Thus, while there is generally an aggregative response onto ephemeral patches of their prey, the numerical response (Section **10.2.3.9**) is restrained by intraspecific effects, as in some bark beetles (Section **4.2.1.2(g)**). Also, sex ratios may be skewed towards spanandry by male-killing *Rickettsia* bacteria (Majerus and Hurst, 1997).

Adults often overwinter in masses in plant debris, occasionally migrating up mountains to do so (Yakhontov, 1962). Like some bark beetles, they may use an assembly pheromone to find each other. Emigration occurs at the end of summer when their food sources are declining, while the reduced temperatures in mountains means that their metabolic rate can be lower than on the plains, hence conserving their metabolic resources. But ladybirds also feed on nectar at this time: I have seen *Adalia* feeding in the UK on ivy flowers in October. After a return migration in spring and before aphids are abundant, pollen, especially that of the Rosaceae, is a major part of their diet. Most ladybirds are conspicuously coloured, usually red or yellow with black markings, which produce strong aposematic patterns (Section **1.4**). Some species secrete a distasteful fluid from special glands in the legs. Not all avian predators, however, are deterred by these devices.

Adults may host larval braconid wasps of the genus *Perilitus*. In Ontario, Canada, *P. coccinellae* is recorded from *Coc. trifasciata* and *Col. maculata* (Smith, 1960). Occasionally, the afflicted beetles survive parasitism (Section **10.2.3.8**). Larvae and pupae are affected by the encyrtid genera *Cowperia* (three species) and *Homalotylus* (>30 species) (Noyes, 2011). Species in *Homalotylus* often parasitize their host during its ecdysis when it is soft and vulnerable. Other hymenopteran parasitoids include *Nothoserphus* spp. (Proctotrupidae), *Pediobius foveolatus* and *Oomyzus scaposus* (Eulophidae), but the first attacks only phytophagous ladybirds. Several species of *Phalacrotophora* (Phoridae) are cosmopolitan pupal parasitoids. Finally, mites such as *Coccipolipus* spp. may infest the sub-elytral space of ladybirds and cause sterility. For much more information on these cute beasts see Majerus (1994), Hodek and Honěk (1996), Obrycki and Kring (1998) and Hodek *et al*. (2012).

Several other beetle families in the Polyphaga have predatory members. The Cleridae often have brightly coloured larvae and contain the genera *Corynetes* and *Thanasimus*, which eat bark beetles, and in North America *Trichodes* larvae are predacious in the nests of bees and wasps (Krombein, 1967). The Lampyridae are the so-called fireflies. Adults are bioluminescent while the larvae feed on a variety of insects and in the case of the European glow-worm, *Lampyris noctiluca*, slugs and snails. In the Silphidae the genus *Xylodrepa* has larvae that eat lepidopteran larvae. In the Rhizophagidae, larval *Rhizophagus grandis* eat scolytid eggs and larvae, having been used to control *Dendroctonus micans* (Section **4.2.1.2(f)**). Another such predator is *Trogossita japonica*, which attacks wood-boring beetles, including *Monochamus* spp. in Japan. Some Cucujid larvae such as *Cucujus* and *Catogenus* are predatory or ectoparasitic on cerambycid pupae, while those of the dermestid beetle *Thaumaglossa* avidly consume the eggs of mantids, chewing through the ootheca.

8.2.2.4(f) LEPIDOPTERA; Geometridae, Lycaenidae. Lepidopterans are unlikely predators, but in Hawaii several geometrid species in *Eupithecia* have raptorial larvae that eat small, soft-bodied insects such as flies, termites and lacewings. Like mantids they are essentially sit-and-wait predators. The whole looping body is used to strike the prey (and would-be parasitoids) and the thoracic legs have long tarsal claws. Many European *Eupithecia* spp. are folivores, or feed on flowers and seeds (South, 1920/1923). The extraordinary divergence of Hawaiian *Eupithecia* from the normal habits of caterpillars cautions one against over-generalization in insect affairs. Then, larvae of the noctuid genus *Eublemma* prey on coccids. Those of some blue butterflies (Lycaenidae), such as *Feniseca tarquinius* in the USA and *Taraka hamada* in Japan (Banno, 1990), eat aphids, and in West Africa *Spalgis* spp. eat mealy bugs. Some lycaenid larvae prey on ants. Final instar larvae of *Maculinea* eat *Myrmica* ants, while in South-East Asia the armoured larvae of *Liphyra brassiolis* prey in all stages on *Oecophylla smaragdina*. In addition, several lepidopteran larvae, such as *Agrotis* and *Heliothis* spp. (Noctuidae), may be cannibals (Fox, 1975).

8.2.2.4(g) DIPTERA; NEMATOCERA; Cecidomyiidae. 4500 species. The larvae of several genera such as *Lestodiplosis* are predators of dipteran larvae and pupae; other genera eat aphids. Of six known parasitoids, *Endaphis pervidus* attacks the aphid *Drepanosiphon*, *Endopsylla agilis* afflicts adult psyllids and *E. endogena* nymphal tingid bugs.

8.2.2.4(h) DIPTERA; BRACHYCERA; Asilidae, Empididae, Dolichopodidae. These families form a group of mainly aerial predators. The Asilidae, evocatively called assassin flies, usually have large adults that feed on a variety of prey, including grasshoppers (Rees and Onsager, 1985), bees, wasps, beetles, butterflies and many Diptera, including tsetse. Large individuals of *Promachus giganteus* in Arizona reach 45 mm in length and 800 mg in mass (Morgan and Shelly, 1988). Asilid larvae are normally predatory in the soil. Adults have large eyes, a dagger-like proboscis and the two front pairs of legs modified for grasping prey. The diverse, natural defences of their prey seem no match for their ravages. They often associate with dry, open areas where they may form isolates of a few hundred individuals. *Machimus atricapillus* is a grey fly ~14 mm long which is common on New Forest (UK) heaths and preys on various insects. Most asilid flies are sit-and-wait predators, generally selecting a perch of dark colour or a stone in a sunlit position, presumably to elevate their T_b. *Asilus* and *Laphira* contain common temperate predators of this type. But the Leptogasterinae typically hunt on the wing, so asilid flies, like dragonflies, show both types of hunting strategy, an example of convergent evolution in divergent orders. Again, as in libellulid dragonflies the thoracic muscles form a high proportion of total body mass, approaching 40% in some species (Marden, 1987). Then in Kazakhstan, *Trichomachimus paludicola* attacks dragonflies much larger than itself. In Arizona, *Efferia tricella* and *Triorla interrupta* have a significant proportion of tiger beetles in their diet (Pearson, 1985). Like the Odonata, larger asilid flies commonly include smaller brethren in their diet (Morgan and Shelly, 1988).

The family is best represented in the tropics (Hull, 1962), where some species of *Hyperechia* aggressively mimic the large carpenter bees *Xylocopa* (Fig. 8.9) on which they prey, while *H. bomboides* develops as an ectoparasitoid of *Xylocopa* larvae. *Dasypogon diadema* eats honey bees in Europe and *Saropogon dispar* does so in Texas, while *Callinicus* preys on solitary bees (*Osmia*, *Andrena*). In the Neotropics, *Dasyllis* aggressively mimics the euglossine genus *Eulaema*. *Maira* and *Lampria* have a metallic coloration, presumably for thermal control (Section **10.2.4.2**). It is possible that these flies inject histolytic enzymes into their prey while feeding, as do carabid beetles. The group has quite a long evolutionary history, some fossil species dating from the Eocene, ~60 Ma.

The other two families comprise generally smaller flies. A few large *Empis* take prey as big as blow flies, but in the main empidid flies capture small Diptera such as mosquitoes and *Simulium*. While they inhabit a variety of ecological situations, they are often found near water. They also eat cereal aphids (Sutherland *et al*., 1987). Some species ambush prey on flowers. *Platypalpus* and *Hilara* contain many small predators. In the former, mid-femora and tibia close like a penknife to hold the prey. Male *H. litorea* lightly wrap a captive, frequently an aphid (Laurence, 1952), in silk and offer it as a nuptial gift. Indeed, similar behaviour occurs in several genera, including *Empis*, *Hilara* and *Rhamphomyia*, a further case where males provide material assistance to the progeny (Section **10.2.5.6**), but also a necessary precaution when being intimate with predatory females.

Fig. 8.9. The asilid fly *Laphria flavicolis*, an efficient aerial predator and aggressive mimic of carpenter bees such as *Xylocopa,* but also preys on several other insects. Source: Wikimedia Commons, author Judy Gallagher.

The generally metallic-green Dolichopodidae, many in the big genus *Dolichopus*, are usually found near water too, or in humid situations where they feed on small insects and their juveniles, such as Collembola, aphids, small Nematocera and other little Diptera. Unlike most flies in the two preceding families their proboscides are short, being surrounded by two grinding plate-like palpi. *Poecilobothrus* adults, who congregate on small shaded pools, can catch mosquito larvae resting at the surface. Several species, including *Thiniphus flavipalpis* and *Hydrophorus oceanus*, are found in salt marshes and other coastal habitats. Some *Medeterus* spp. and the empidid fly *Tachypeza* rarely fly, but are running hunters on tree trunks and walls where they capture Collembola, thrips and small Diptera. *Tachypeza nubila* establishes temporary hunting areas (Nicolai, 1986). Larval *Medeterus* live under bark and may feed on bark beetle larvae. Indeed, most dolichopodid larvae are thought to be carnivores. *Scellus notatus* is an impressive little predator with raptorial fore legs. The males of many species are memorable for their relatively huge genitalia, the donkeys of the insect world (Fig. 8.10). Not content with this, several species have adornments on their antennae and their fore or mid-tarsi. *Argyra diaphana* males form mating swarms, traversing the forest floor, their silvery backs showing intermittently.

8.2.2.4(i) DIPTERA; CYCLORRHAPHA; Syrphidae.

These attractive insects form a scion at the base of cyclorrhaphan evolution. Larval **Syrphinae** are generally voracious if unlikely predators of aphids, other soft-bodied homopteroids and small caterpillars (Schneider, 1969). Unlikely, since they lack eyes and legs. Eggs are laid near aphid colonies, being stimulated by the honeydew (Carter and Dixon, 1984). The young, greenish larvae creep on adhesive, ventral welts, probably locating their prey by chemosensory means. On finding an aphid, a larva plunges its mouth hooks into the prey and, lifting it clear of the plant, sucks out the haemolymph. In Europe and elsewhere, numerous species of *Syrphus*, *Episyrphus*, *Metasyrphus*, *Paragus, Platychirus, Melanostoma, Scaeva, Sphaerophoria* and *Baccha* have predatory larvae of this type. In UK wheat fields, *Syrphus ribesii, S. corollae, S. nitidicollis, E. balteatus, Sc. pyrasti* and several *Platychirus* spp. are abundant, where they consume *Sitobion* and *Metapolophium* aphids (Section **5.3.1.2**(**h**)). They are active in early summer, when most needed in agriculture. A larva often consumes >400 aphids during its development, while *S. corollae* may eat >850. *Pipeza* and *Heringia* oviposit on the galls of *Pemphigus* (Section **3.3.3.1**(**a**)), their larvae consuming the contents (Schneider, 1969). In New Zealand and elsewhere, syrphine larvae prey on young caterpillar pests of brassicas, including *Pieris* and *Plutella* (White *et al*., 1995). In Europe, the numbers of adults generally peak in May, but they need a ready supply of pollen if they are to function effectively in integrated pest management (IPM) systems (Section **13.3.1**). Some species are long-distance migrants, and return autumn migrations of 'hundreds of thousands' of *Episyrphus balteatus* have been caught in a Swiss mountain pass together with numerous *Syrphus corollae*, *S. vitripennis*, *Melanostoma mellinum* and *Sphaerophoria scripta* (Schneider, 1969).

Fig. 8.10. Male *Dolichopus ungulatus* (Dolichopodidae). These flies are rather small, running predators on plants. Again, the metallic coloration thwarts over-heating. Source: Wikimedia Commons, author Martin Cooper.

There is some evidence that a few *Catabomba* species may occasionally be parasitoids (Colyer and Hammond, 1951). But syrphine juveniles are host to several ichneumonid, figitid and encyrtid wasps (Rotheray, 1984). For example, the abundant *S. ribesii* is afflicted by *Diplazon pectoratorius* and *Syrphophilus tricinctorius* (Ichneumonidae) and *Callaspidia defonscolombei* and *Melanips opacus* (Figitidae). Adult *Eristalis tenax* (Eristalinae), whose larvae inhabit putrid waters, is an efficient pollinator (Rader *et al*., 2009). Indeed, many other species in this and other sub-families probably pollinate as they commonly feed at flowers. A little up the classification, among numerous families of acalypterate flies, the Chamaemyiidae is a small group whose larvae eat aphids, thus *Leucopis pemphigae* feed on *Pemphigus betae* fundatrigenae in Canada (Harper, 1963).

8.2.2.4(j) DIPTERA; CYCLORRHAPHA; Cordiluridae.

This family, transitional between the Acalyptratae and the Calyptratae, contains the dung flies *Scopeuma* (= *Scatophaga*). *Scopeuma stercorarium* is common in Europe and North America, where the adults attack soft-bodied insects, particularly Diptera, either those visiting dung or feeding at blossoms. They possess a non-rigid, retractile proboscis armed with prestomal teeth for this purpose. Males are larger than females and may prey on them, refreshingly different from what occurs in many predatory insects. They mate and oviposit on fresh cow dung, and are often found in large numbers. Larval development takes place in the dung and pupation beneath it. Localities where cattle are pastured contain large populations of this fly, which must therefore exert great predatory pressure on other insects, especially Diptera. Such prey include biting stable flies (*Stomoxys*) and their relatives (Section **7.3.2.4(o)**), which are a constant nuisance to livestock in summer.

8.2.2.4(k) DIPTERA; CYCLORRHAPHA; Muscidae. This diverse family has some genera with carnivorous larvae that eat larvae of other Diptera living in carcasses, faeces, rotting wood or fungi. They are found in *Fannia, Graphomya*, *Muscina*, *Morellia, Mycophaga, Mydaea, Phaonia* and *Polietes*. It is less well known that genera such as *Coenosia, Lispe* and *Paraprosalpia* have adults that eat adult Diptera. For example, *Lispe tentaculata* is a common predator along British seashores (Colyer and Hammond, 1951). The family also contains a few parasitoids (Section **8.2.2.5(i)**).

8.2.2.4(l) HYMENOPTERA; APOCRITA; Formicidae. Like the social wasps (Section **8.2.2.4(l)**) the social structure and co-operative behaviour of ants is dependent to a great extent on the genetic affinity of the females. It is a huge family with many predatory species and scavengers of dead insects although some more highly evolved genera like *Pheiodole* have become vegetarian or like *Atta*, fungivorous. Ecitonnine, doryline, ponerine and some formicine ants exert constant predatory pressure on other insects, especially in the Neotropics (Dyer, 1995), where scarcely 1 m^2 of any surface is free of a questing ant. In Brazilian selva, Fonseca and Ganade (1993) estimated the density of *plants associated* with ants to be ~380/ha. This involved 16 plant and 25 ant species. Here, *Eciton* driver ants patrol the forest floor eating everything they can overpower, even lizards and small mammals. Ants provide a rare case of co-operative predation in insects, a common behaviour in predatory mammals. In *Eciton* (Fig. 8.11), the marching columns may be >200 metres long, comprise half a million workers and can be observed close up if you tread judiciously! Similarly, the African species of *Dorylus* may have several million members in their marauding hoards. Their passage means death for animals that cannot move out of their way. Both groups are effectively blind, so that the pattern of foraging is mediated by tactile and chemosensory means. Many tropical ponerine ants eat termites. In Jamaica, *Crematogaster brevispinosa* frequently usurps their arboreal nests. In temperate regions, *Formica* contains many predatory species that consume large quantities of herbivores. Hunters from a big nest of *F. rufa* may eat more than half a million caterpillars per year, while *F. yessensis* is a significant predator of such beasts on chaparral oaks on the coast of Hokkaido (Ito and Higashi, 1991). Interestingly, those exposed on leaves had higher mortality than those in spun refuges within or between leaves.

Fig. 8.11. Driver ants, *Eciton burchellii* (Formicidae) from Amazonia, foraging on the forest floor. Source: Wikimedia Commons, author KatzBird.

Ants, especially in the Formicinae and Dolichoderinae, show non-predatory relations with several aphidid, membracid and coccid bugs. For example, some species of *Lasius* imbibe honeydew from them, protect them from predatory insects and move them to new feeding sites. In some *Acropyga* the queen transports a few scale insects on her nuptial flight as ‘seed’ parents. In *Prenolepis,* a swollen ant morph or ‘replete’ stores the honeydew, regurgitating it to larvae and to sister ants (Wilson, 1971). Then, the association of ants with homopteroid bugs may have consequences for other insects in the same patch. Thus, ant/aphid associations on poplars have marked effects on such insects, more species being found on trees lacking these associations (Wimp and Whitham, 2001). So they are a major part of interaction webs (Section **10.1.2**).

Indeed, a variety of other insects associate with ants and frequently employ chemical mimicry to deceive them (Liepert and Dettner, 1993; Dettner and Liepert, 1994). Many that penetrate social insect colonies have the same cuticular hydrocarbon profile as that of their host. Aphidiine wasps that specifically parasitize aphids tended by ants often employ such deception. The ants not only protect the aphids, but also their parasitoids! Such chemically based mimicry has like complexity to that mediated by reflected light (Sections **5.2.1.3(b)** and **10.2.3.5**). In that involving *Aphis fabae*, the ant *Lasius niger* and the aphidiine wasp *Lysiphlebus cardui*, many major and minor peaks of cuticular hydrocarbons correspond in their respective gas chromatograms (Liepert and Dettner, 1996). For a general study of these important and unusual insects, see Hölldobler and Wilson (1990).

8.2.2.4(m) HYMENOPTERA; APOCRITA; Vespoidea. Social and solitary wasps also exert considerable predatory pressure on other insects. Vespid and eumenid wasps particularly target caterpillars. In temperate regions, *Vespula* is the major genus, while *Vespa*, the hornets, are large and formidable predators (Matsuura and Yamane, 1984). In the Himalayas, *Vespula ducalis* queens reach 40 mm in length. In the Caribbean, species of *Polistes* have become semi-domesticated, building their open-celled nests under the eaves of houses and rarely stinging people unless carelessly provoked. But in tropical South American forests the situation is far different. Some *Polybia, Synoeca* and *Cartergus* will stream 20–30 m from their nests and attack you. Many genera are arboreal and require special collection methods for detailed population studies (Freeman, 1973b). Some such nests are encased in mud. In the Amazonian forest, huge paper nests of *Polybia dimidiata* are built low down around sapling trees. In 1967, O.W. Richards, Ian Bishop and I found that their nests might contain <40,000 workers, being the most dangerous objects in the area, especially since nests are often paired. Collecting them is a true story rivalling a Bruce Willis action film.

8.2.2.4(n) HYMENOPTERA; APOCRITA; Sphecoidea, Sphecidae. The sub-families of these solitary wasps are often specialized predators of specific groups, which the females collect and paralyse as larval food to stock their cells. They have especially acute vision (Land, 1997). Most Pemphredoninae prey on aphids and other homopteroids, while the Crabroninae collect small Diptera. In the Sphecinae, *Sphex* captures Orthoptera and *Ammophila* kills caterpillars, burying them in nests in the soil. Pantropical and Mediterranean *Sceliphron* build mud cells for the progeny, stocking them with orb-web, thomisid and jumping spiders. In Jamaica, a large female of *S. assimile* will provision >100 such spiders during her 3-week life span and kill and feed on many more (Fig. 8.12; Freeman and Johnston, 1978a). While the Nyssoninae collect a variety of insects, *Bembix* selects large Diptera including the tachinid fly *Echinomyia,* and also *Tabanus* and *Glossina*. In southern states of the USA, *B. carolina* hunts tabanid and other flies that come near horses and is known as the 'horse guard'. The large (25–38 mm long), spectacular *Sphecius speciosus* captures cicadas. The Philanthinae include the 'bee wolves', which paralyse bees and feed them to the larvae. In several sphecid genera, for example, *Ampulex, Larra, Philanthus, Stizus* and *Tachysphex*, a venomous 'cocktail' of proteins, peptides and sub-peptides is injected into their prey (Libersat *et al.*, 2009). While not killing them, the victims are rendered harmless while the wasp provisions them fresh to the larvae.

8.2.2.5 Parasitoids

Parasitoids, like predatory insects, do an immense job in reducing the numbers of other insects, although not all populations are so affected, especially those in the soil. While they afflict predatory insects, not just herbivores and detritivores, they form much of our biocontrol armoury. All are Endopterygota (Godfray, 1994). Because exopterygotes (Section

Fig. 8.12. Spider-hunting wasps *Sceliphron destellatorium* (Sphecidae), close relatives of *S. assimile,* mentioned in the text frequently. Source: Wikimedia Commons, author Gail Hampshire.

1.2.2) have no pupal stage of change, the highly modified lifestyle of a juvenile parasitoid may be incompatible with development into an active, sentient, adult female. This idea, however, being untestable, is pure conjecture (Popper, 1989; Section **11.5.1**). But many external larval parasitoids exist: *Hyperechia bomboides* (Asilidae) on *Xylocopa* larvae, *Melittobia* (Eulophidae) on wasp larvae, and *Larra* (Sphecidae) on mole crickets, and it is a fact that there are no exopterygotes among them.

Adult parasitoids are often predatory, generally on the same population(s) of victims (Section **8.2.2.1**; de Bach, 1943; Jervis and Kidd, 1986; Jervis *et al*., 2001). For example, female *Tetrastichus asparagi* feed on young eggs but oviposit in those with a developed embryo, having the effect of allowing fewer hosts to be available for later parasitism (Godfray and Muller, 1998), although this may not be limiting. Also, the AF of a parasitoid is broadly related to the risk that the progeny experience (Price, 1973, 1997), being greater in those that oviposit in young juveniles than in old ones. Naturally, the size of a parasitoid wasp depends to an extent on the size of its host, but this can be devalued if it places more than one offspring per victim (Traynor and Mayhew, 2005). For example, solitary parasitoids typically deposit a single offspring per host, while gregarious ones deposit several. This may present a conflict of interest: it can be to the female's advantage to deposit more progeny than the latter would prefer (Waage, 1986). *Endoparasitoids* consume their hosts from the inside (*endophagous*), usually devouring non-vital organs like the fat body and/or haemolymph first. *Ectoparasitoids* feed from the outside of their hosts (*exophagous*), often when these are enclosed in burrows, mines and galls. Both may do so in the company of siblings. Ectoparasitoids generally have longer handling times (Section **11.5.2.3**) than endoparasitoids do as they have both to subdue and oviposit on their victims (Gauld and Bolton, 1991). Even so, the former may be competitively superior when attacking the same host (Gross, 1991).

Some parasitoids kill or permanently paralyse their hosts quickly (*idiobionts*), while others (*koinobionts*) live within them for an extended period (Askew and Shaw, 1986). Salt (1968) pointed out that 'carnassial' parasitoids attack and kill their victims rapidly whereas others develop slowly and insidiously. The latter thereby usurp the host's natural defence strategies and hence benefit from its continuing life, but will die if the host dies. Unsurprisingly, the carnassial species or idiobionts usually attack endophytic victims, where they can continue to feed in comparative safety. Koinobionts on the other hand, more frequently attack exophytic victims (Hawkins *et al*., 1990). An idiobiont killing an externally feeding caterpillar that fell to the ground would have scant chance of survival itself. Even so, when a host is parasitized it may have less chance of survival anyway, as in experimental groups of pea aphids attacked by *Aphidius ervi* (Ives and Settle, 1996) and in cannibalistic *Cephus* larvae. Endophagous parasitoids, unless carnassial species, must cope with the internal immune reactions of their hosts, which are mediated by the haematocytes. Since developing insect eggs have no or few haematocytes they have little immunity. Indeed, the effectiveness of a host's immune system increases during juvenile development with the increasing number of haematocytes. Some koinobionts oviposit in eggs that continue to develop in host larvae, a strategy perhaps permitting gradual adaptation to their immune system. When such wasps, for example, the ichneumons *Hyposoter exiguae* and *Bathyplectes curculionis*, lay eggs in larger larvae they are often encapsulated (Puttler, 1969; van den Bosch, 1964, in Salt, 1968), providing early data that *only some hosts are killed by being parasitized.* So the idea that a host is doomed when a parasitoid oviposits in it is naïve, for frequently it recovers. Long ago, Strickland 1923 (in Salt, 1968) found that young larvae of *Gonia capitata* (Tachinidae) were often encapsulated by its cutworm host before they could seek a safe place in its brain. In an extreme case, only 1% of the eggs of *Asobara tabida* survive in the larvae of *Drosophila melanogaster* (van Alphen and Visser, 1990; Section **10.2.5.2**). But when hosts recover from parasitoid attack they may be sterile or less fecund (Section **10.2.5.6**), as in the larch sawfly attacked by the ichneumon *Mesoleius* (Section **5.2.1.3**(**e**)). Then, when *Thelairia bryanti* (Tachinidae) parasitized the larvae of the arctiid moth *Platyprepia virginalis* adult moths, fertile eggs and flies resulted (English-Loeb *et al*., 1990). Also, survival from parasitism of its polyphagous caterpillars varied with their food plant, being highest on poison hemlock (Karban and English-Loeb, 1997). DeVries (1984) found a similar example in butterflies.

Idiobionts include many exophagous forms, koinobionts are mainly endophagous. Since the latter have a long-lasting and intimate relationship with their hosts, their host ranges should be restricted (Askew and Shaw, 1986), as the parasitoids must adapt to and combat the host's immune systems. Tests of this hypothesis with the chalcidoid parasitoids of arboreal leaf miners in the UK, and with the ichneumons of Canadian forest insects (Sheehan and Hawkins, 1991), give strong support for it. But there is much variation. In addition, there is a tie-up between these different developmental strategies and pro- and synovigeny (Section **10.2.5.1**). Although pro-ovigenic parasitoids are few, they are associated with koinobiosis (Jervis *et al*., 2001). Such females spend longer as pupae, tend to be short-lived as adults and lay numerous small eggs that have little yolk.

The defences of potential hosts against parasitoids share parallels with those of plants against herbivores (Section **2.4.2**) and of mosquitoes killing *Plasmodium* (Section **7.3.2.4(d)**). In all cases there is a potential for escape in space and time. For secondary defences there are also superficial physical barriers, such as the thick exoskeleton in beetles and cocoons surrounding some pupae (Strand and Pech, 1995). Ectoparasitoids are outside the ambit of the host's physiology, but a parasitoid inside its host faces a range of tertiary defensive measures. These can be separated as *natural* and *acquired immunity*, a division rather like that of *pre-existing* and *induced defences* in plants. But the basic, frequent host response is a co-ordinated mass attack from its haematocytes, which attempt to encapsulate the intruder. These cells recognize it as *non-self*, adhere to it, form the capsule and kill it. Similarly, some strains of *Anopheles gambiae* kill their protistan parasites and then encapsulate them in melanin. But endoparasitoids have evolved many co-ordinated counter measures. Some apparently hide from the haematocytes within host organs, while some tachinid larvae enter ganglia, salivary glands or flight muscles, and/or modify encapsulation for their own ends (Salt, 1968). *Exorista* larvae modify the capsule into a respiratory funnel (Valigurová *et al*., 2014). Others avoid encapsulation by failing to elicit the host's immune response, probably by molecular mimicry – natural deception (Sections **10.1** and **10.2.3.5**) at the biochemical level. In the Ichneumonoidea, however, sophisticated mechanisms have evolved (Section **8.2.2.5(k)**).

It often happens that ovipositing females fail ostensibly to recognize that a host is already parasitized, which may result in *superparasitism* (Fiske, 1910). Early workers saw this as a failure to discriminate a parasitized host, either by self or by a conspecific female, from an unparasitized one. Later it was found to be an adaptive strategy (van Alphen and Nell, 1982; Weisser and Houston, 1993). In solitary parasitoids only one parasitoid larva can mature, so when there are two, a mortal struggle ensues. In such species young larvae are often equipped with relatively massive mandibles, as in *Microctonus* (Section **6.2.1.2(a)**), used to kill any competitor. If these larvae are siblings, little increased RS to the mother and her mate can accrue from superparasitism; but if they are non-siblings there can be a chance of winning and hence increased RS (van Alphen and Visser, 1990). Conversely, superparasitism may help to suppress the host's immune system (Waage, 1986). When the parasitoids are of different species, good competitors should not shun competition. But in many parasitic wasps, females mark the host, and even the patch, with a deterrent pheromone. Although wasps often discriminate and avoid a host that is already parasitized, this ability is poorly developed in tachinid flies (Caron *et al*., 2010).

When a potential host, whether pest or not, extends its range, maybe due to climatic changes, it is often met with attack from parasitoids with wide host ranges. These have, so to speak, added the alien to their list of victims. When the leaf mining gracillariid moth *Phyllonorycter leucographella* recently extended its range from Turkey to Scotland, it was attacked by 14 new parasitoid species on the way (Gröbler and Lewis, 2008).

Recall (Section **8.2.2.1**) that parasitoids of other parasitoids are termed hyperparasitoids. Those that lay eggs only in other parasitoids are *obligate hyperparasitoids*. Those that also operate as primary parasitoids are *facultative hyperparasitoids* (Sullivan, 1987). They may attack a primary parasitoid directly by laying an egg in or on it, or indirectly when they oviposit in or on *the host* of the primary parasitoid. In all, they have a wider range of victims than primary parasitoids do (Gordh, 1981, in Sullivan, 1987). Hyperparasitoids are common in the Hymenoptera (Ichneumonidae, Eulophidae, Encyrtidae, Pteromalidae and Cynipidae), in a few Diptera (Bombyliidae, Conopidae) and Coleoptera (Cleridae) (Borror *et al*., 1989; Sullivan and Völkl, 1999). They add complexity to life by comprising a fourth trophic level. They possibly evolved from ectoparasitoids (Godfray, 1994), since no special adaptations are required to oviposit and feed on primary parasitoids as well as on primary hosts. But several evolutionary routes may exist. Instead of simply killing a competing endoparasitoid, becoming its hyperparasitoid might lead to a more efficient use of resources. Hyperparasitoids may even attack each other, providing yet another trophic level. Life table work on the field dynamics of parasitoids is sparse, to say the least (Freeman and Ittyeipe, 1993; Section **11.4.4.1**), that on hyperparasitoids is possibly non-existent.

The major sections of parasitoids are in the Diptera (Brachycera and Cyclorrhapha; ~16,000 species) and in the Hymenoptera (Parasitica and Aculeata). The Parasitica alone contains >300,000 described species and without doubt many more undescribed ones. But before dealing with them, there are a few curious parasitoids to note in three other endopterygote orders. For further information see Salt (1968), Askew (1971), Waage and Greathead (1986), Hawkins and Cornell (1994), Godfray (1994), Feener and Brown (1997) and Quicke (1997).

8.2.2.5(a) NEUROPTERA; Mantispidae. The larvae of different mantispid species, whose adults are predatory (see Fig. 8.7), are often parasitic (~50 species) on spider's eggs or, very differently, on the larvae of solitary wasps. A species of *Plegia* attacks the prepupae of *Typoxylon palliditarse* in Trinidad (Freeman, 1981a).

8.2.2.5(b) COLEOPTERA; Rhipiceridae, Cucujidae, Rhipiphoridae, Meloidae. Including those in the Carabidae and Staphylinidae, there are ~4000 parasitoid species described from the Coleoptera. The Rhipiceridae (~200 species) contains the genus *Sandalus*, which are little-known parasites of cicada nymphs. In the Cucujidae the larvae of some species of *Catogenus* parasitize cerambycid larvae under bark in broad-leaved forests. In the Rhipiphoridae (~400 species) the larvae afflict various wasps and bees. In North America, *Macrosiagon* parasitizes solitary wasp larvae within their cells (Krombein, 1967), while in Europe *Metoecus paradoxus* attacks ground-nesting *Paravespula*. Similarly, *Rhipiphorus* spp. associate with solitary bees. *Cerocoma* favours grasshoppers that have been captured and provisioned by the solitary wasp *Tachytes*, namely the predator has already done the dirty work for the parasitoid. *Rhipidius quadriceps* is an endoparasite of the forest cockroach *Ectobius*. Similarly, *R. pectinicornis* develops in *Blatella germanica*.

The members of the Meloidae (~2000 species) commonly afflict grasshopper egg pods and ground-nesting bees and wasps. Females lay huge numbers of eggs (~2000–10,000) that hatch into mobile, minuscule campodeiform larvae called *triungulins*. These are sometimes transported on male bees, transfer to the females during copulation, and eventually gain access to the nest where they eat the eggs and the bee bread provisions. Species of *Meloe* are parasites of bees including *Halictus, Andrena, Osmia* and *Chalicodoma*. Again, *Nemognatha* spp. are associated with solitary bees (Krombein, 1967). *Lytta* (formerly *Cantharis*) and *Mylabris*, popularly known as 'Spanish flies', are used to produce cantharidin, a pharmaceutical product. But *L. vesicatoria* develops in the nests of the leaf-cutter bees *Megachile*, among other genera.

8.2.2.5(c) STREPSIPTERA; Stylopids. Peculiar parasitoids of a few, diverse insect groups; ~550 species. This is a small, anomalous order sometimes placed as a superfamily in the Coleoptera. A few species develop in Thysanura, but the majority attack Exopterygota: gryllid and mantid orthopteroids, and pentatomid and delphacid bugs, including *Nilaparvata lugens* (Section **5.3.1.2(d)**), but also wasps and bees. For example, *Xenos* attacks *Polistes* wasps, while *Pseudoxenos* affects solitary wasps. Male adults have mesothoracic halteres and metathoracic wings, but are otherwise beetle-like. They are intensely active for just a few hours and then die. Mature female Strepsiptera project from their host but do not leave it and if fertilized, produce thousands of minute, ambulatory, triungulin larvae, rather resembling those of meloid beetles (Section **8.2.2.5(b)**).

8.2.2.5(d) DIPTERA. While there are a few odd parasitic Cecidomyiidae, for example *Endaphis pervidus* a parasitoid of the aphid *Drepanosiphon*, the bulk of dipteran parasitoids are in the Brachycera and Cyclorrhapha. The latter sub-order contains the large, interesting and important family **Tachinidae**, which, although lacking hyperparasitoids, is notable for the wide range of hosts attacked. Both dipteran and hymenopteran parasitoids, being active insects, are sensitive to bad weather when searching. Rates of parasitism are likely to be suppressed in such weather.

8.2.2.5(e) DIPTERA; BRACHYCERA; Bombyliidae. 3000 species. These are medium to large, hairy, ectoparasitic flies with a fossil record going back to the Oligocene. Adult *Bombylius* aggressively mimic various solitary bees and parasitize their larvae. Various species attack *Andrena*, *Halictus* and *Colletes*. In these parasitoids, thread-like first larval instars, rather like those of some Tachinidae, seek out the host. *Anthrax* and its relatives attack a variety of other insects including lepidopteran larvae, parasitic ichneumonid, tachinid and cicindelid larvae, grasshopper egg pods and some solitary wasp larvae. In Jamaica, *Anthrax irroratus* afflicts the larval bees of *Megachile zaptlana* and *Chalicodoma lanata* (Raw, 1984). *Villa hottentotta* parasitizes larvae of the pine beauty moth, while *Hemipenthes maurus* is a hyperparasitoid within these caterpillars, attacking for example the tachinid fly *Ernestia rudis* and the ichneumon *Ophion*. In the USA, *Systoechus vulgaris* is a common parasite of grasshoppers. The related family Cyrtidae (= Acroceridae) contains endoparasitoids of spiders.

8.2.2.5(f) DIPTERA; CYCLORRHAPHA; Phoridae, Pipunculidae. 3000 species. The biology of phorid flies has been poorly researched until recently (Disney, 1994), possibly due to their unprepossessing appearance. *Pseudacteon* and *Aenigmatias*, however, parasitize ant genera such as *Lasius* and *Formica*. In Texas, *Apocephalus* parasitizes the large soldiers of *Pheidole dentata* preferentially, so reducing the colony's defences against the aggressive ant *Solenopsis texana* (Feener, 1981). They are well represented in the Neotropics: *A. paraponerae* lives in the head capsule of the giant ant *Paraponera,* which it decapitates prior to pupation. Other *Apocephalus* spp. attack leaf-cutter ants. *Solenopsis geminata* is host to an amazing number (21) of *Pseudacteon* species (Plowes *et al*., 2009). Some species of the big genus *Megaselia,* such as *M. rufipes,* although normally saprophagous, may be facultative parasites on adult grasshoppers and immature Lepidoptera and Coleoptera (Colyer and Hammond, 1951; Zvereva and Rank, 2003). Others attack tipulid larvae and coccinellid prepupae (Eggleton and Belshaw, 1992). In all, parasitic phorid flies affect insects associated with the ground (Feener and Brown, 1997).

Adult Pipunculidae (600 species) are small but have relatively large heads comprised mainly of eyes, with specialized frontodorsal areas in the females that provide enhanced resolution (Land, 1997). They also have independently evolved ovipositors. They often hover delicately between foliage and, like the Conopidae (Section **8.2.2.5(g)**), may parasitize their hosts while flying (Feener and Brown, 1997). The larvae are mainly endoparasitoids of the Auchenorrhyncha, especially the Cicadellidae, Cercopidae and Delphacidae. For example, *Verrallia aucta* afflicts 'cuckoo-spit' insects (Cercopidae) in England (Whittaker, 1971), laying eggs in the abdomen of the adult.

8.2.2.5(g) DIPTERA; CYCLORRHAPHA; Conopidae. 800 species. In contrast to the Phoridae, genera in this group are often big and beautiful flies (*Conops*, *Leopoldius*, *Myopa, Physocephala*, *Sicus* and *Zodion*). They have endoparasitic larvae that afflict mainly a variety of adult bees and wasps, which the adults may mimic aggressively. As in some pipunculid parasitoids, conopid flies generally oviposit in flight, attaching an egg within or on their adult host. *Physocephala* and *Sicus* are common on *Bombus* in Switzerland (Schmid-Hempel and Schmid-Hempel, 1988). They attack workers visiting flowers, inserting single eggs though an intersegmental membrane. Strangely, *Trifolium* pollinated by parasitized *Bombus* workers set heavier seed than those pollinated by unparasitized ones (Gillespie *et al*., 2015). *Bombus* queens cease foraging too early to be at risk. As in many tachinid flies, the larvae fix their posterior spiracles to the host's tracheal system, so obtaining gaseous exchange. Parasitized bees normally die within 2 weeks, their life expectancy being reduced. But their behaviour changes: they seek cool micro-environments and often bury themselves before succumbing. Pupation is within the cadaver. High levels of parasitism in a colony result in smaller queens whose chance of founding a nest in the following year is reduced. *Psithyrus* bees (Section **8.2.2.5(z)**) are not parasitized, however, possibly because they have a tough integument (Goulson, 2003).

Females of the Neotropical *Stylogaster* hover over the foraging columns of the driver ants *Eciton* (Section **8.2.2.4(k)**; see Fig. 8.11) and, diving like Stuka bombers in WWII, oviposit on cockroaches flushed from the jungle floor. Their eggs, which have a harpoon tip, stick into the cockroach's waxy cuticle, but they may also be attached to the tachinid flies *Calodexia* and *Androeurops* that are also engaged in parasitizing the cockroaches (Gotwald, 1995). Meanwhile, wingless diapriid wasps run among the ants, mimicking their behaviour and probably parasitizing their juveniles (Godfray, 1994): a veritable microcosm of complex entomology.

Another small family is the **Nemestrinidae**. These flies can be significant parasitoids of rangeland grasshoppers in North America (Laws and Joern, 2012). Among other such flies, the wingless *Braulus* (Braulidae) is carried phoretically by honey bees, their larvae consuming the stored pollen. Then some species in the **Chloropidae** are parasitic; thus, *Gaurax* develops in the egg sacs of spiders, while others are found in locust egg pods.

8.2.2.5(h) DIPTERA; CYCLORRHAPHA; Tachinidae. ~10,000 species. This family dates from the Eocene, and while largely endoparasitic (Askew, 1971), it has diverse and interesting habits. These flies exert a major influence on the dynamics of many Lepidoptera, some Diptera and Coleoptera, and a few Hemiptera and orthopteroids. But the majority attack larvae on plants (Stireman *et al.*, 2006); their old name being Larvaevoridae. On occasion, however, their maggots are found in adult hosts, as in the bugs *Nezara* and *Eurygaster*, and may be transported with them (Section **10.2.5.7**). Some young tachinid larvae avoid the host's defences by entering organs such as the fat body, muscle, glands and neural tissue, or by completing their early development in its gut. Tachinid biology is best viewed in terms of tritrophic co-evolution (Section **9.8**).

Although worldwide in distribution, they are especially speciose in the Neotropics. In rain forests there they cause ~46% of all parasitism on caterpillars (Gentry and Dyer, 2002). About 100 species have been used in biocontrol, many successfully. They are diurnally active, look alert and usually medium-sized bristly beasts (**Fig. 8.13**) with a rapid bustling flight like blow flies. Indeed, associative learning occurs in *Drino bohemica* (Monteith, 1963, in Arthur, 1966). *Taxonomically*, there are four sub-families: Exoristinae, Dexiinae, Phasiinae and Tachininae, and over 50 tribes. *Behaviourally*, four groups can be recognized according to their mode of *egg distribution* (Section **10.2.5.2**). This classification, modified from Pantel (1910), reflects the evolution of an increasing ability of adult females to seek and find their hosts (ISC; Section **10.2.4.1**) instead of leaving numerous progeny to do so. But the taxonomic and behavioural groups do not tie up directly. Behavioural evolution, at least partially, has taken place *within* each subfamily (**Table 8.1**), rather as in the evolution of zygomorphic flowers in several orders of dicotyledons (Cronquist, 1988). Even so, egg scattering and/or having numerous mobile larvae (groups 1 and 2) are successful strategies: ~40% of adult Palaearctic Tachinidae do not seek close contact with hosts. In general, tachinid flies lack the offensive weapons that Parasitica use to subdue hosts, nor do they often feed on them (but see group 4); they do, however, have a similar range of egg-laying tactics to the Parasitica (cf. Section **8.2.2.5(q)**), and also, one presumes, ovarian modifications for doing so.

Fig. 8.13. The tachinid fly *Archytas apicifer.* Its numerous eggs hatch to give mobile, searching triungulins. Source: Wikimedia Commons, author Melissa McMasters.

Group 1. Very large numbers of minute, *microtype* eggs are scattered over the plant food of their caterpillar hosts, who may swallow them. These eggs contain little yolk, relying on nutrition within the host to sustain embryogenesis (Wheeler, 1996). In any case large eggs could not be swallowed. This strategy, like that in group 2, also allows access to hosts that the adult female, due to her large size, cannot reach. But many such species attack perfectly accessible exophytic caterpillars. In some cases, as in *Blepharipa pratensis* on gypsy moths and *Cyzenis albicans* on winter moths, females are first attracted to chewed foliage. In several such species AF may be >12,000. If the eggs are ingested undamaged they hatch in the host's gut. The parasitoid larvae eventually migrate to the feeding site, although young larvae may hide in the host's organs so avoiding attack by the haematocytes (Section **8.2.2.5**). This group includes *Salmacia*, whose victims are usually noctuid moths and other Lepidoptera, but also the ground-nesting bees *Bombus* and *Anthophora*. It also includes *Zenillia* and *Sturmia*, *S. sericariae* being a parasitoid of *Bombyx mori*. In *C. albicans*, females require ~1 month to mature the eggs (Hassell, 1969), during which time pre-reproductive mortality occurs

Table 8.1. Reproductive strategies in some genera of tachinid flies.

Strategy	Exoristinae	Dexiinae	Phasiinae	Tachininae
Egg scatterers	*Cyzenis* *Phasmophaga* *Anisia*			*Salmacia*
Eggs give triungulins		*Dexia* *Dexiosoma* *Trixa*		*Ernestia* *Varichaeta* *Meriania* *Echinomyia* *Gymnocheta* *Archytas*
Egg stickers	*Exorista* *Compsilura* *Winthemia* *Eucelatoria*			*Nemorilla* *Phryxe* *Crocuta* *Voria*
Eggs injected	*Phorocera*		*Alophora* *Paralophora* *Weberia*	

(Section **10.2.3.1**). In his study, only a small proportion of the eggs was ingested, but these had to be eaten by larger larvae to have a chance of survival. Of the ~1500 eggs a female might lay, only ~3–50 survived to adulthood, according to season.

Group 2. Quick-hatching eggs or ambulatory, host-seeking larvae (triungulins) are deposited in places likely to be inhabited by the host, especially if hidden in stems and fruits (Clausen, 1940). Triungulins are covered in hard plates, perhaps reducing predation and desiccation. The numerous genera include *Echinomyia*, *Ernestia*, *Gymnocheta*, *Lixophaga*, *Meriania* and *Varichaeta*, which all attack lepidopteran larvae. *Dexia* and *Dexiosoma* oviposit on the ground, their larvae seeking cockchafer grubs. *Popillia japonica* larvae may be heavily parasitized by such larvae (Rikhter, 1975, in Brown and Gange, 1990). Similarly, *Trixa caerulescens* larviposits on dung, its triungulins seeking larval beetles. Both groups 1 and 2 practise *indirect oviposition*, the former of minute, numerous, undeveloped eggs; the latter with eggs of variable size, number and hatching rate (Stireman *et al*., 2006), the triungulins often finding inaccessible hosts (Feener and Brown, 1997).

Group 3. Females locate each host and attach a large, *macrotype* egg to it. When the larva hatches it bores into its host and finds the feeding site. Numerous genera here include *Compsilura, Exorista, Parasetigena*, *Phryxe*, *Nemorilla, Thebaira*, *Voria* and *Winthemia*, most of which attack lepidopteran larvae, and *Bucentes* (= *Crocuta*), which also attacks *Tipula* larvae. *Crocuta cristata* is reported as a parasite of the semi-aquatic larvae of *T. Acutipula maxima*, and, like its host, pupates in soil. In a sample of 212 larvae from nine species of *Tipula* from the New Forest, Hampshire, and from Kent, UK, only members of this sub-genus were so parasitized (Freeman, 1967b). *Exorista larvarum* and *Compsilura concinnata* are used in the biological control of defoliating moths in North America. Both attack a wide range of hosts. *Voria ruralis* is abundant in the UK, its gregarious larvae being found in those of several butterflies and moths, including the pest *Mamestra brassicae* (Section **5.2.1.4(m)**).

Group 4. Again, females locate hosts themselves and, using a special spine or ovipositor, insert an egg or larva. Eggs hatch quickly and larvae move to the feeding site. In groups 1 and 2 AF is much greater than in groups 3 and 4, in which there is *direct oviposition* and AF is <600 (Stireman *et al*., 2006). *Weberia*, which attacks adult carabid beetles, and *Ocyptera* belong here. Strangely, in *Alophora hemiptera* the males, which are much larger than females, have the general shape of a smooth pentatomid bug that the females parasitize. Its status as an aggressive mimic (Section **10.2.3.5**) is questionable. Female *Eucelatoria bryani* larviposit in *and feed on Heliothis* larvae. The latter behaviour, which often occurs in parasitic wasps (Section **8.2.2.1**), greatly increases the fly's AF (Nettles, 1987). *Winthemia rufopicta* oviposits *on Heliothis zea*, but nearly all the eggs laid on penultimate instar larvae and up to 50% of those on final instar larvae are moulted off before they hatch (Danks, 1975, in Gross, 1993).

Concerning biocontrol, Greathead (1986) quotes 35 cases of effective control by 30 different tachinid species. While the main problem is getting them to mate in culture, they often spread rapidly when released. *Gonipterus scutellatus*, introduced to control eucalyptus snout beetles, was found over 150 km distant after 1 year (de Bach, 1974). They have been especially useful in controlling Lepidoptera, although less so than the parasitic Hymenoptera, but of course they represent only a single family. Examples are *Euphasiopteryx* (= *Ormia*) *depleta* on mole crickets, *Trichopoda* spp. on *Nezara viridula*, *Bessa remota* on coconut moths, *Winthemia rufopicta* on *Heliothis* spp. and *Cyzenis albicans* on winter moths in Canada (Section **5.2.1.4(g)**). *Compsilura concinnata*, a widespread and highly generalist parasitoid, not only suppresses gypsy moth populations but also attacks some 200 other species, including Hymenoptera and Coleoptera (Stireman *et al*., 2006).

8.2.2.5(i) DIPTERA; CYCLORRHAPHA; Calliphoridae (including Sarcophaginae), and two unusual parasites in the Muscidae. Parasitic species are mainly in the Sarcophaginae (~1250 species). *Brachycoma devia* is a parasite of *Bombus* species in Europe, especially the common carder bee, *B. agrorum*, while in North America *Br. sarcophagina* behaves similarly. In the latter, larviparous females deposit progeny within the nest. The fly larva feed only after its host spins a cocoon. Other sarcophagid parasitoids of *Bombus* are *Boettcharia litorosa* and *Helicobia morionella* (Schmid-Hempel, 1998). *Taxigramma* and *Blaesoxipha* are endoparasitoids of Orthoptera, *Noditermitomyia* of termites, and *Agria* of larval Lepidoptera. Several species attack earthworms or terrestrial gastropods. *Miltogramma* comprises the 'satellite flies', so named because a female will follow a potential solitary wasp host back to its nest, flying some 30–40 cm behind it, as if invisibly attached. Laden, slow-flying *Sceliphron* females so followed will generally drop their prey and shake off *Miltogramma*. Successful sleuths, however, wait motionless near the nest until the coast is clear and then lay several eggs in the open cell that is being provisioned (personal observation). The larvae consume the provisions, kill the host and may spread to other cells. *Metopia* similarly attacks the nests of ground-nesting bees and wasps.

Stomorhina lunata is parasitic on the egg pods of desert and migratory locusts (Section **5.2.1.1**) on which they lay eggs. The occasional presence of the fly in temperate Europe may mean that it also attacks grasshoppers, *or* that it has made a long-distance migration. In West Africa, *Blaesoxipha* is a major parasitoid of *Zonocerus* (Section **5.2.1.1(f)**). When *Colcondamyia auditrix* is attracted by the calls of its cicada host (Section **3.3.2(a)**), only males are normally parasitized, and, because they remain silent subsequently, they are not parasitized again, presumably another case of behavioural manipulation. *Emblemosoma* is another genus favouring cicadas.

In the Muscidae, Anthomyiinae the aberrant genera *Acridomyia* and *Tettigoniomyia* are parasitic on acridid and tettigoniid grasshoppers, respectively. The females penetrate their host with their *mouthparts* and insert eggs (Eggleton and Belshaw, 1992). Recall that some weevils use these organs to insert eggs into plants.

8.2.2.5(j) HYMENOPTERA; PARASITICA. The Hymenoptera, both parasitoid and predatory (Section **8.2.2.4(k)** to **8.2.2.4(m)**), have the greatest number of aggressive associations with other insects (Schoenly, 1990). This is generally regarded as an outcome of the evolution of their ovipositor from its original plant-slashing role in the Symphyta to its use as a mobile sting in the Apocrita (Malyshev, 1968; Whitfield, 1998; Pennacchio and Strand, 2006). In Parasitica, it is a sophisticated structure with serrations hardened with heavy metal–protein complexes, internal channels that deliver venom and internal sculpturing to aid passage of the egg (Sivinski and Aluja, 2003). Apart from having this critical organ and its associated venom glands, these wasps are haplodiploid, allowing females to control sex ratio in the progeny. Haplodiploidy may also result in reducing population variability (Graur, 1985). The group has an ancestry of ~160 Ma (Whitfield, 1998) and contains the large majority of all insect parasitoids (Doutt, 1959). Parasitic wasps are implicated in a major part of all successful biocontrol programmes. As in the Tachinidae, classifying their life-history strategies in relation to taxonomy would help us to understand these fascinating insects. The main trend (Table 8.2) is from ectoparasitic idiobionts to endoparasitic koinobionts, but excepting the Platygasteroidea, a single

Table 8.2. Reproductive strategies in superfamilies of the Parasitica.

	Ectoparasitoids	Endoparasitoids
Idiobionts	Evanioidea (part) Ichneumonoidea (part) Chalcidoidea (part)	Platygasteroidea (part)
Koinobionts	Chalcidoidea (part)	Evanioidea (part) Ichneumonoidea (part) Chalcidoidea (part) Platygasteroidea (part) Cynipoidea (part) Proctotrupoidea (all)

behavioural strategy is not confined to particular superfamilies, rather as in the Tachinidae.

While there are numerous families, we deal below with those in the two largest superfamilies first. These are the structurally more primitive, generally larger, long-legged group, the Ichneumonoidea, and the structurally more advanced, smaller and more compact Chalcidoidea. Ichneumonoids have quite complex wing venation and long, filamentous antennae, while chalcidoids have simple venation and generally elbowed antennae. Ichneumonoid larvae spin cocoons, which protect them in various ways, while chalcidoid larvae generally do not. Recent analysis shows an affinity between the Ichneumonoidea and another group, the Evanioidea, and through to the Aculeata (Pennacchio and Strand, 2006), with the remaining superfamilies forming a second clade.

The types of *egg distribution* found in parasitic wasps parallel those found in tachinid flies (Section **8.2.2.5**(**h**)), there being *indirect* and *direct* oviposition. In the Trigonalidae and Eucharitidae each female scatters 5000 or more eggs in the probable vicinity of a potential host. The trigonalid genus *Poecilogonalus* has 450 ovarioles/ovary and can deposit >10,000 eggs in 2 weeks (Wheeler, 1996). *Mantibaria manticida* (Scelionidae) deposits eggs on the egg mass of *Mantis religiosa*. In parasitoids with exophagous larvae, like *Melittobia*, eggs are attached to the host's body surface. But many families inject eggs into the host. As in tachinid flies, AF is related to egg distribution, being less when oviposition is direct. But relative size of the victim can also be a factor. In *Melittobia* >500 eggs may be laid on a single, relatively enormous, aculeate larva such as *Zeta* (Fig. 8.14). Far fewer are laid on little wasps (*Pachodynerus*) and fly puparia (*Amobia*, *Neobellieria*) (Thompson and Parker, 1927; Freeman and Ittyeipe, 1993; Silva-Torres and Matthews, 2003), and by virgin females (Abe *et al*., 2010).

Fig. 8.14. Final instar *Melittobia* larvae massed on the surface of their *Sceliphron* host. Reproduced with permission courtesy of Jeff Hollenbeck.

The mode of reproduction varies greatly in Hymenoptera and in Parasitica in particular, but males are always haploid and impaternate. Females are diploid and either biparental or uniparental (Flanders, 1945; Richards and Davies, 1988). In the latter case (*theletoky*), known in >20 families, females lay female eggs without mating. Recall that this happens in vine weevils (Section **3.2.1.2**(**c**)). In some species uniparental and biparental reproduction occur in separate geographical races. But such variation can be seasonal, theletoky being associated with low temperature and suggesting that the sexes are able to meet less often in inclement weather. In some braconid, encyrtid and platygasterid wasps, fertilized eggs continue to divide to produce a clone of up to 2000 offspring, the process of *polyembryony*. Then, changes in sex ratio may result from bacterial interference in the internal affairs of the wasp, the microbe being vertical transmitted in the egg cytoplasm. Application of an antibiotic kills these bacteria and novel emergence of males occurs (Stouthamer *et al.*, 1990, 1993). Even the host's food can affect the sex ratio of emerging parasitoids. When red scales (Section **6.3.2.2(a)**) feed on yucca, the sex ratio of their parasitoid, *Comperiella bifasciata*, was 84% female, whereas it was 45% when they fed on orange (Smith, 1957). Such features and like variants complicate the dynamics of Parasitica, especially as envisaged in models (Section **11.5.2.3**). Another complicating feature is that females short of food resorb the eggs, and in *Pimpla* even wing muscles. In *P. turionellae,* energy and materials from this thoracic source are probably used in oogenesis (Jervis and Kidd, 1986), as is known in some bugs and beetles (Section **10.2.5.2**).

8.2.2.5(k) HYMENOPTERA; PARASITICA; Ichneumonoidea. ~150,000 species. These wasps can be divided into two groups. Ichneumonidae (*ichneumons*) are generally larger, with an abdomen longer than the head and thorax combined, and often possess a long ovipositor. Braconidae are often smaller and somewhat stouter, have slightly less complex wing venation (Matthews, 1974) and usually short ovipositors. Unlike ichneumons, the Braconidae are never hyperparasites (Sullivan, 1987). Both groups have been used extensively in biocontrol. In ichneumons, 45 species in 30 genera have become established, giving control in 22 cases. In the Braconidae these data are 66 species in 23 genera and 53 cases (Greathead, 1986), with *Apanteles* (= *Cotesia*) alone being successful against some 14 pests. Ichneumons are very effective in controlling sawfly larvae, while braconid wasps are better against lepidopteran larvae. In a Neotropical rain forest, braconid wasps had attacked 31% of all parasitized lepidopteran larvae (Gentry and Dyer, 2002).

In ichneumons, Price (1973), following Iwata (1955), describes an interesting and basic relationship between AF and risk to progeny. Fecundity, measured by the number of ovarioles in the ovary (Section **10.2.5.1**) varies widely, from ~5 in Ichneumoninae to ~50 in Eucerotini, while a strong negative relationship exists between ovariole number and ovipositor length (Price, 1973). Price points out that wasps having long ovipositors would take longer to find and parasitize their hosts, and so do not need abundant eggs. There is also a correlation between expected host mortality (and therefore that of the juvenile parasitoid) and fecundity. Young hosts are more numerous and so more easily found than old ones, but die more often. This is far different, however, from *Melittobia's* case (Freeman and Ittyeipe, 1993). In wide-scale field studies in Jamaica, its AF averaged 300–500, but juvenile mortality only ~25%, >93% of the progeny being female. The population equation here balances only if there are huge losses of females during dispersal and migration (Section **10.2.4.8**).

While both families possess >50,000 species, the ichneumons are thought to be more diverse in temperate regions (Owen and Owen, 1974). Related to this, one of their major host groups, the Symphyta, is scarce in the tropics. Because many lepidopteran larvae are better defended there by allelochemicals from their food, this may cause ichneumons attacking them to be less numerous (Gauld *et al.*, 1992; Sime and Brower, 1998), supporting the '*nasty host hypothesis*'. This suggests that herbivores defend themselves from parasitoids, as well as from predators, by this means (Section **10.2.3.8**). Furthermore, rhyssine ichneumons, which attack wood-boring larvae that are hence undefended by allelochemicals, are species rich in tropical forests. Similarly, all egg parasitoids (eggs are poorly defended) are also species rich in the tropics (Gauld *et al.*, 1992). The caveat here is that nearly all tropical insects are poorly studied.

But more is to come. At Cambridge University (UK) George Salt pioneered research into the mechanisms used by ichneumons to suppress the immune responses of their hosts. He showed that as the eggs of *Venturia* (= *Nemeritis*) passed through the calyx region of its reproductive tract, they gained a translucent coat *outside* the chorion. This contained 'very numerous particles, ~1300Å in diameter' (Salt, 1968). Later on, in both ichneumonid and braconid wasps, they were identified as symbiotic viruses (Stoltz and Vinson, 1979). They are now termed polyDNAviruses (PVs), bracoviruses (BVs) and ichnoviruses (IVs) (Turnbull and Webb, 2002; Kroemer and Webb, 2004). These wasps inject special venoms into their host along with the egg(s). But PVs are confined to only three ichneumonid sub-families (Banchinae, Campopleginae and Ctenopelmatinae) and to the microgasteroid complex in the Braconidae. Even so, they exist in some 30,000 species. Both viral groups, while morphologically different in the two wasp families, ultimately suppress encapsulation, the host's usual defence against all foreign bodies, parasitoids and all (Edson *et al.*, 1981; Godfray, 1994; Strand and

Pech, 1995; Section **8.2.2.5**). The evidence is that these viruses do not have a genome *per se*, rather their DNA is part of the wasp's genome (Federici and Bigot, 2003), who suggest therefore, that PVs are actually wasp organelles, and so the Polydnaviridae should be disestablished.

Comparative studies on the BV genomes of three *Microplitis* spp. show that rapidly evolved differences affect the host specificity of these braconid wasps (Kadash *et al*., 2003, in Kroemer and Webb, 2004). This is perhaps tripartite co-evolution in which the PVs are mutualistic with parasitoids and pathogenic to hosts (Fleming, 1992). In braconid wasps, another mechanism in this arms race is the injection of special cells, 'teratocytes' (Hollande, 1920; Salt, 1968). These are usually derived from polar bodies and so are maternal. Initially they suppress the host's immune responses, but later may have a nutritive function, as in the anucleate sperm of *Manduca sexta* (Section **5.2.1.4(h)**) and some butterflies (Trivers, 1985), for the maturing larva often eats them. In addition, there may be a biochemical disguise of the egg surface (Wharton, 1993), and it is significant that the first larval instar may grow considerably within the protective chorion. These mechanisms are maternal investments in the success of the progeny (Section **11.2.3**), and hence her own RS.

Equivalent mechanisms are strangely unreported in the Chalcidoidea, which is, nevertheless, a huge group (Strand and Pech, 1995; Turnbull and Webb, 2002; Drezen *et al*., 2003). However, an apparent RNA virus is transmitted vertically by the cynipoid parasitoid *Leptopilina* (Figitidae) and probably suppresses the immune system of its *Drosophila* host (Rizki and Rizki, 1990, in Federici and Bigot, 2003). Then in the Platygasteroidea, several species of *Platygaster* produce 'pseudogerms', whose origin and function may be compared to those of teratocytes (Salt, 1968).

8.2.2.5(l) HYMENOPTERA; PARASITICA; Ichneumonoidea; Ichneumonidae. Important sub-families here are the Ephialtinae, with the genera *Ephialtes*, *Rhyssa*, *Megarhyssa* and *Thalessa* (Fig. 8.15), that attack the larvae of wood-boring insects, including those of *Sirex* and *Tremex*, and of big Coleoptera. In these large ichneumons the ovipositor may be pushed >10 mm into the wood to effect parasitism. *Rhyssa persuasoria* females often mutually contest an area of infested trunk. In the Tryphoninae and Scolobatinae *Polyblastus* and *Pleolophus* parasitize sawflies, while *Lathrolestes marginatus* helps to control apple sawflies in Eastern Europe (Blommers, 1994). The Ichneumoninae and Ophioninae specialize on lepidopteran larvae. *Ophion* spp. are nocturnal, orange/brown, have large eyes and are known in Jamaica as 'night wasse'. They often attack noctuid larvae including cutworms. In North America, *Thyreodon atriclor* parasitizes sphingid larvae while *Glypta rufiscutellaris* affects Oriental fruit moths (Section **6.3.1.1(h)**). Other groups include the Porizontinae on larval Lepidoptera (*Phobocampe disparis* parasitizes gypsy moths; Section **5.2.1.4(f)**), Microleptinae on fungus gnats and Diplazontinae on Syrphinae. For example, *Diplazon laetatorius* attacks species in *Episyrphus*, *Syrphus*, *Platychirus* and *Melanostoma*. Tersilochinae specialize on beetles. *Tersilochus conotracheli* parasitizes plum curculios (Section **6.2.1.2(d)**), *T. microgaster* afflicts *Psylliodes chrysocephala* (cabbage stem flea beetles) and *T. obscurator* attacks *Ceutorhynchus pallidactylus* (cabbage stem weevils) (Barari *et al*., 2005). Hence, parasitoid sub-family in ichneumons often relates to host taxon.

Fig. 8.15. The ephialtine ichneumon *Rhyssa persuasoria* that parasitizes large boring larvae, such as *Sirex*, deep in heartwood. Such larvae are probably located by the sounds or vibrations they make while chewing.

8.2.2.5(m) HYMENOPTERA; PARASITICA; Ichneumonoidea; braconidae. Braconid wasps may be better adapted to warm, dry conditions than are ichneumons. But like them the numerous braconid subfamilies tend to be host specific at an ordinal level (Matthews, 1974; Wharton, 1993). While a majority of species lays one egg per host, others like *Apanteles* lay several. The sibling larvae are mutually non-aggressive and often pupate *en masse* in white or sulfur-yellow cocoons adorning the dead victim (Fig. 8.16). *Syntretus splendidus* is another such parasitoid of *Bombus* and *Psithyrus*. While lability exists in braconid taxonomy (Wharton, 1993), the following will serve as a brief introduction to their diversity.

The Helconinae are probably primitive and seek wood-boring larval beetles. The Microgasterinae parasitize lepidopteran larvae and contains the big genus *Apanteles*. *Apanteles* (= *Cotesia*) *glomerata* attacks *Pieris* while *A. medicaginis* infests *Colias philodice* butterflies. In European IPM apple orchards, *A. ater* combats tortrix moths. *Apanteles flavipes*, introduced to several Caribbean islands, controls the cane borer *Diatraea*, while in East Africa it has been partly successful in suppressing a variety of lepidopteran borers in cereals. Its success may stem from its behaviour of entering the borer's tunnels. It also indulges in sib mating which mitigates any Allee effect (Section **10.2.2.4**). In New Zealand, *A. ruficus* controls the cutworm *Mythimna separata*. In North America, *A. congregatus* attacks hawk moth larvae, including those of *Manduca*. In the Braconinae, *Bracon mellitor* parasitizes *Anthonomus grandis* (Section **6.2.1.2(c)**) and caterpillars such as *Heliothis*. Other braconine genera afflict sawfly larvae. In the Euphorinae, *Microctonus* is memorable in its attack of *adult* ground beetles, flea beetles and weevils. In *M. aethiopoides* the ovaries contain special ascovirus-like virions thought to immunosuppress these hosts. *Dinocampus coccinellae* is a global parasitoid of adult ladybirds and has also been found in *Sitona* weevils. Similarly, *Perilitus* attacks adult *Hylobius* pine weevils. The Adeliinae, Agathidinae, Cardiochilinae, Cheloninae, Macrocentrinae and Rhogadinae also mainly affect lepidopteran larvae and Meteorideinae their pupae. The Cardiochilinae oviposit in lepidopteran eggs, but continue development in larvae. In Spathiinae, *Spathius* attacks bark beetles, Ichneutinae sawflies, while Alysiinae and Opiinae, together comprising >2300 species, afflict cyclorrhaphan Diptera.

Fig. 8.16. Braconid larvae having bored out of a hawk moth larva have pupated in cocoons on its surface. Many species of braconid larvae have such behaviour. Source: Wikimedia Commons, author Stsmith.

The Aphidiinae are often given family status and attack aphids specifically (Starý, 1970). Do not confuse Aphidiinae, which are wasps, with Aphidinae, which are aphids. *Aphidius* spp. are often found in adult, migrant *Sitobion avenae*, getting a free but risky ride. Several species including *Aphidius colemani, A. ervi* and *A. matricariae* are available commercially for biocontrol (Powell and Wright, 1988). *Diaeretiella rapae* and *Lysiphlebus testaceipes* are major parasitoids of cereal aphids in the Great Plains, the former also attacking cabbage aphids. Some *Lysiphlebus* spp. engage in chemical deception, for unlike *Trioxys* they are unmolested by ants attending the aphids (Völkl, 1992). Their deception is due to mimicry of cuticular hydrocarbons (Liepert and Dettner, 1996; Section **10.2.3.5**). Aphidiine females lay single eggs in nymphal aphids, but hosts do not succumb until adult (koinobiont). Here and in the related *Diaeretus* and *Trioxys* pupation takes place within the host's body, while in *Praon* it occurs beneath it. Parasitized hosts inflate and turn straw-brown (mummies), making them conspicuous. Emerging *Praon* cut an opening like a tiny trap door, leaving a specific trace event. Such entomological minutiae, trivial in themselves, can provide workers on population dynamics with long-lasting traces of short-term events, ones valuable in constructing life tables (Section **11.4.2**).

In the UK, *Aphidius rhopalosiphi, A. ervi* and *A. picipes* attack *Sitobion avenae* on wheat. The last named wasp, as *A. avenae*, was found in 1860 by John Curtis. *Aphidius uzbekistanicus* afflicts aphids on barley, while *Toxares deltiger* is a fairly recent discovery. Some *Aphidius* spp. can overwinter inside cereal aphids, continuing to develop above a threshold of ~7°C (Vickerman, 1982a), may move around inside them and carry hyperparasites (Walton *et al*., 2011). In southern UK adults may emerge in March, providing an early brake on aphid population growth. *Aphidius* spp. are hyperparasitized by *Dendrocerus* spp. (Megaspilidae). Generally, however, aphidiine larvae of several species, like *Microctonus* larvae in weevils, are often transported by their alate hosts to new habitats. This occurs in *Aulocorthum* *solani* on potatoes, *Metopolophium festucae* on wheat, *Brevicoryne brassicae* on crucifers and *Myzus persicae* on several crops (Walton *et al.*, 2011).

8.2.2.5(n) HYMENOPTERA; PARASITICA; Chalcidoidea. This is a huge group of ~100,000 species (Pennacchio and Strand, 2006), but it is next to certain that the majority is yet to be described. They are more evolved structurally than the ichneumonoids, but average only 2–3 mm in length, although many, especially the egg parasitoids, are smaller. They are often metallic green (Willmer, 1982; Section **10.2.4.2**). The wings, which have reduced venation, are usually carried flat over the back when not in use. While most species are parasitoids or hyperparasitoids, several in the Agaontidae (fig-insects), Torymidae, Perilampidae, Eurytomidae and Pteromalidae are herbivores, either infesting seeds or forming galls (Richards and Davies, 1988). Hypermetamorphosis, the existence of several larval forms in an individual, is frequent. Except in *Euplectrus*, cocoons are unknown. Some of the important families are considered below.

8.2.2.5(o) HYMENOPTERA; PARASITICA; Chalcidoidea; Trichogrammatidae, Mymaridae. These families comprise >2000 world species. They afflict insect eggs and are hence very small indeed: some *Alaptus* spp. are <0.25 mm in length. It is incredible that the basic insect structure can be so miniaturized. In the Trichogrammatidae, *Trichogramma evanescens* is a much-studied, ubiquitous species that parasitizes a wide variety of insect eggs (Thompson and Parker, 1928a). In the USA, *T. minutum* is employed widely for biocontrol and *T. pretiosum* has been used against *Heliothis* on cotton and the gelechiid moths *Phthorimaea* and *Tuta* on tomatoes (Pratissoli and Parra, 2000). Some *Trichogramma* use sex pheromones adhering to plants to detect the proximity of potential hosts (Noldus *et al.*, 1991, in Vet and Dicke, 1992). But insect eggs are not entirely defenceless against these mini-destroyers. Commonly, the chorion hardens as it ages, increasingly resisting penetration, and there are wide differences between host species (Pak *et al.*, 1990, in Gross, 1993). Potential hosts are progressively protected and handling times (Section **11.5.2.3**) increased, a further factor in biocontrol. In Europe, apterous females of *Prestwichia aquatica* search under water for eggs of aquatic beetles and bugs. *Caraphractus cintus* similarly parasitizes *Dytiscus* and dytiscid eggs (Jackson, 1958). Other trichogrammatid species attack beetle and moth eggs in stored products. In the **Mymaridae**, too, several species are used for biocontrol: *Anagrus atomus* and *A. epos* for leafhoppers, *A. pseudococci* for mealy bugs and *Anaphes iole* for *Lygus* bugs. Because they operate early, agents killing eggs reduce crop losses from the juveniles of many phytophagous pests. Limited evidence (Jervis *et al.*, 2001) suggests that while trichogrammatid wasps are synovigenic, mymarid wasps are pro-ovigenic (Section **8.2.2.5**).

8.2.2.5(p) HYMENOPTERA; PARASITICA; Chalcidoidea; Eulophidae (including Aphelinidae). >3000 species. This large and diverse family often shows strong sexual dimorphism. About 50% ($n = 113$) of all cases of effective biocontrol by parasitoids employed this family (Greathead, 1986). Several genera affect leaf miners with *Diglyphus*, *Cirrospilus*, *Horismenus,* and *Tetrastichus* containing parasites of citrus leaf miners (Section **5.2.2.1(c)**). Recently in Taiwan, *T. brontispae* suppressed populations of coconut leaf beetles *Brontispa longissima*. *Tetrastichus asparagi* is a gregarious egg parasitoid of asparagus beetles, *Crioceris asparagi* and *C. unidecim-punctata*. In Jamaica, *Chrysonotomyia* spp. parasitize the eggs of the giant swallowtail *Papilio homerus,* destroying up to 65% of them. *Entedon* spp. attack the larvae of *Apion* spp. (Section **6.2.1.2(a)**), whereas *Pediobius foveolatus* attacks bruchid beetles. *Hemiptarsenus anementus* is a parasitoid of leaf mining sawflies. *Eulophus larvarum* live gregariously inside caterpillars, pupating radially around the cadaver. *Colpoclypeus florus* is used against tortrix moths in European IPM apple orchards, but like *Diadegma*, the ichneumon of diamond-back moths (Section **5.2.1.4(a)**), it needs a separate host that overwinters in the larval stage.

Aphelinus, *Aphytis*, *Coccophagus* and *Encarsia*, often separated in the Aphelinidae, are well known parasitoids of aphids, whiteflies and scale insects. *Encarsia formosa* (Section **10.2.1**) is usually parthenogenetic, a condition caused by *Wolbachia* (Section **10.2.3.9**). The wasp, which has two strains, is used extensively to control Trialeurodes whiteflies attacking in greenhouse crops. Originally discovered by an observant Hertfordshire, UK, gardener in 1926 (van Emden and Service, 2004), the species' potential was realized by staff of the Cheshunt Research Station where they bred it for use in greenhouses in the Lea Valley close by, which at that time supplied London with vegetables. Other species used in biocontrol in greenhouses are

E. tricolor and *E. pergandiella*. *Aphytis* spp. have been employed successfully in the control of red, purple, olive and mussel scales. In South Africa, *Aprostocetus ceroplastae* is a major parasitoid of the citrus scale *Ceroplastes* destructor. Other eulophid wasps are hyperparasitoids. In Africa and the Mediterranean Basin, *Marietta exitiosa* attacks parasitoids within a variety of scale insects and psyllid bugs (Kfir *et al.*, 1976). In *Coccophagus*, females develop in scale insects, but male larvae are hyperparasitoids within the same group.

In contrast to most of these parasitoids, *Melittobia australica* lays all of its several hundred eggs on a single host, generally a late larval solitary wasp or bee. Both adult females and larval progeny feed externally on the host and slowly kill it. With extreme spanandry (Hamilton, 1967), the few apterous males are very pugnacious (Matthews *et al.*, 2009; Innocent *et al.*, 2011), fighting their brothers to the death for the privilege of mating with their sisters and never leaving the host's cells. Then there are three female morphs in *M. australica*, each of which is modified for different search distances (Freeman and Ittyeipe, 1982, 1993; Section **10.2.4.8**). Crawlers and jumpers remain in the patch, while fliers, the majority, search the landscape.

8.2.2.5(q) HYMENOPTERA; PARASITICA; Chalcidoidea; Encyrtidae. >3000 species. Again, the large family Encyrtidae specializes in parasitism of aphids and other small homopteroids, although some Lepidoptera are also attacked. Sixty-one species in 34 genera have been used in 53 cases of effective biocontrol (Greathead, 1986). *Metaphycus bartletti*, *M. helvolus* and *M. lounsburyi* are used commercially to control scale insects, as are *Apoanagyrus lopezi* and *Leptomastix dactylopii* for mealy bugs. *Microterys flavus* is a cosmopolitan, gregarious parasitoid of soft scale insects (Kfir *et al.*, 1976). A few of these wasps, such as *Cheiloneurus*, are hyperparasitoids and others exhibit polyembryony. For example, *Copidosoma trucatellum* oviposits in cabbage looper eggs (Section **5.2.1.4(m)**), frequently laying two eggs, an unfertilized male egg and a fertilized female egg. Each undergoes polyembryony, dividing into numerous individuals, which soon become male or female larvae. The looper's egg changes into a larva that develops to maturity, so feeding and sheltering a mass of 1000–3000 minute parasitoids. *Copidosoma koehleri* has similar biology and is used against the potato tuber moth *Phthorimaea operculella*. *Holcothorax testaceipes* afflicts leaf mining *Phyllonorycter* in European IPM apple orchards. *Ooencyrtus kuwanai* has been employed to control gypsy moths (Section **5.2.1.4(f)**), and in Hawaii and Mauritius *O. erionotae* attacks the banana skipper, *Erionota thrax*. Other *Ooencyrtus* spp. are recorded from *Papilio* spp. eggs (Fig. 8.17). *Ooencyrtus trinidadensis* and *O. fariai* are used against the triatomine vectors of Chagas' disease (Section **7.3.1.1**). The related Eupelmidae contains genera with a wide range of hosts. *Anastatus* is an egg parasitoid of *Nezara* in Hawaii and *Eupelmus* attacks bruchid larvae (Doury and Rojas-Rousse, 1994), whereas others exploit gall-forming sawflies (Askew and Shaw, 1986).

8.2.2.5(r) HYMENOPTERA; PARASITICA; Chalcidoidea; Eucharitidae. Eucharitidae is a small, mainly tropical family comprising relatively large, metallic or black wasps. Eggs are usually scattered on leaves near the host and produce *planidia* larvae, recalling the strategy used by some tachinid flies. As in such flies, AF may be extremely high (15,000/female). Planidia seize ants and ultimately parasitize ant pupae within their nests. *Orasema* attacks the tropical ant *Pheidole*, but also *Solenopsis*, an invasive pest ant in the USA. All instars employ chemical deception to invade these nests (Dettner and Liepert, 1994).

8.2.2.5(s) HYMENOPTERA; PARASITICA; Chalcidoidea; Pteromalidae. >3000 species. Pteromalid wasps are small, often glossy black or metallic green. They parasitize a wide range of hosts, several species being used in biocontrol. On occasion they eat

Fig. 8.17. An adult parasitoid wasp emerging from the egg of a stink bug. Source: US Department of Agriculture, photographer Brian T. Cutting.

plants. *Heydenia unica* parasitizes the bark beetle *Phloeosinus dentata,* while *Anisopteromalus calandrae* and *Choetospila elegans* attack larval beetles in stored products. The bright green *Pteromalus puparum* lays several eggs in the pupae of *Pieris* butterflies. Each emerging parasitoid chews its own hole, leaving perforated remains that are diagnostic. *Dibrachys boucheanus* afflicts several insects that form small cocoons, often those of ichneumonid or braconid wasps such as *Apanteles*, so operating as a hyperparasitoid. *Pachyneuron concolor* is a cosmopolitan, polyphagous hyperparasitoid attacking encyrtid wasps in a variety of hosts: soft scales, mealybugs, aphids and coccinellid larvae (Sullivan, 1987). In South Africa, however, *Trichilogaster* feeds on acacias (Section **8.2.3**).

8.2.2.5(t) HYMENOPTERA; PARASITICA; Chalcidoidea; Eurytomidae, Chalcididae, Leucospididae. The Eurytomidae includes the seed chalcids, which are mainly phytophagous. *Bruchophagus* infests clover and lucerne seeds, while *Harmolita* forms stem galls in cereals and grasses. But many species are parasitic, especially on gall-forming insects. *Rileya*, for example, attacks gall midges and *Eurytoma* a wide variety of insects. Adults in this family and in the Chalcididae have greatly enlarged hind femora. There are several chalcidid hyperparasitoids that attack tachinid flies and ichneumonid wasps. Even so, some of them are of medium size. *Spilochalcis mariae* attacks the pupae of large silk moths and several species of *Chalcis* affect moth pupae, but also the maggots of cyclorrhaphan Diptera.

The Leucospididae are large, striking black and yellow wasps that parasitize Aculeata, so being aggressive mimics. The ovipositor sheath extends dorsally over the abdomen as far as the thorax. *Leucospis affinis* has been bred from the nests of leaf-cutter bees, although the bees themselves are brown! This may be *aide mémoire* mimicry in which potential victims gain protection by reminding potential predators of past failures. They need not *exactly resemble* a noxious or dangerous prey, it is adequate if the enemy recalls a disagreeable result of a past failed assault (Rothschild, 1984; Section **10.2.3.5**).

8.2.2.5(u) HYMENOPTERA; PARASITICA; Evanioidea; Evaniidae, Aulacidae. 1200 species. The **Evaniidae** contains the distinctive ensign wasps that wave their abbreviated abdomen, borne high on the thorax by a slender petiole, like a flag. The friendly *Evania appendigaster* parasitizes cockroach oothecae and is often seen in kitchens in the tropics on its way to seek its *Periplaneta* hosts where the human eye cannot see. *Brachygaster* and *Hyptia* spp. attack woodland cockroaches in Europe and North America, respectively. The Aulacidae have genera that are endoparasitic koinobionts of larval buprestid and cerambycid beetles.

8.2.2.5(v) HYMENOPTERA; PARASITICA; Cynipoidea (4000 species); Cynipidae, Ibaliidae. Most Cynipidae gall plants, especially oaks (oak apples) and roses (ragged robins). But the Charipinae contains hyperparasitoids of *Aphidius* spp. attacking aphids and the Eucoilinae mainly parasitize juvenile Diptera. *Trybliographa* (= *Cothonaspis*) *rapae* attacks cabbage root flies (Section **3.2.2.1**(**i**)) and *Eucoilia eucera* frit flies (Section **4.4.1.1**(**g**)). In the small family Ibaliidae, *Ibalia leucospoides* parasitizes *Sirex* larvae.

8.2.2.5(w) HYMENOPTERA; PARASITICA; Proctotrupoidea. 10,000 species. Several families. The Proctotrupidae are medium-sized, endoparasitic koinobionts that generally attack Diptera or Coleoptera. *Phaenoserphus viator* has been found in carabid (Critchley, 1973) and elaterid larvae. The Pelecinidae are specialist parasitoids of melolonthine larvae in the soil. In *Pelecinus polyturator,* females have a very elongated abdomen that is used to locate their hosts, but they have no sting. The Heloridae is a small, widely distributed family that parasitize Chrysopidae (Section **8.2.2.4**(**a**)), and so are enemies of enemies, perhaps 'hyper-enemies'. Further complexity occurs in the Ceraphronidae, a group best known as hyperparasitoids of braconid and chalcid parasites of aphids. For example, *Lygocerus* are ectoparasites of *Aphidius* living within the aphid.

The Scelionidae are speciose, widely distributed and attack eggs of moths, bugs and Orthoptera. *Telenomus* spp. are found in the eggs of several forest moths: *T. heliothidis* attacks *Heliothis virescens* (Section **6.2.1.2**(**d**)) and *T. remus* has been used against *Spodoptera* in Barbados. *Trissolcus basalis* can control *Nezara viridula* (Section **6.3.2.1**(**a**)) in the Australasian region. *Mantibaria manticida* females live as ectoparasites on preying mantids. When their host oviposits they lay their own eggs in the egg mass of the mantis, these becoming endoparasitic idiobionts. *Mantibaria* on a male mantis decline and die without progeny (Richards and Davies, 1988). We noted the depredations of *Scelio* on locust egg pods (Section **5.2.1.1**(**a**)) and that of

Eumicrosoma on the eggs of *Blissus* (Section **5.3.1.1(a)**). *Sinoditella bisulcata* lives like a louse on grasshoppers in the Caribbean. It waits to oviposit until its host lays its egg pod. Finally, the Platygasteridae are mainly minute and black, often laying eggs in those of their host. However, these hatch in the host's larva and may exhibit polyembryony. They are frequently endoparasitic koinobionts, especially of gall midges. *Platygaster hiemalis* is used to control Hessian flies, while *Amitus* spp. are employed against whiteflies.

8.2.2.5(x) HYMENOPTERA; ACULEATA; Bethyloidea; Chrysididae. Cuckoo wasps. ~3000 species. In aculeate females the egg canal is separate from the sting, the original ovipositor, and thus free to evolve as a specialized offensive weapon. The eggs are laid external to the host (Pennacchio and Strand, 2006). Cuckoo wasps, Chrysididae, lay eggs in the completed cells of solitary bees and wasps. The parasitic larvae attack mature host larvae and/or the provisions. The adults are medium-sized (8–12 mm), bright metallic blue, green or even red, with a thick, coarsely sculptured integument, which may protect them from aggressive host adults. When attacked they often roll up into a ball and drop. In the UK, *Chrysis ignita* feeds on caterpillars stored in the cells of *Odynerus*. In Jamaica, a species of *Hexachrysis* occasionally attacks the larvae of *Sceliphron assimile*. In the Bethylidae, *Cephalonomia tarsalis* affects the saw toothed grain beetle (Section **6.3.1.2(k)**), laying a male and a female egg together on the host larva (Powell, 1938).

8.2.2.5(y) HYMENOPTERA; ACULEATA; Scolioidea; Mutillidae and Scoliidae. Velvet ants and wasps. This superfamily is related to the ants. In these two memorable families of parasitoids, the females deposit eggs externally on the host and their larvae are external parasites. Female Mutillidae, the velvet ants, are apterous (males are winged), possess a formidable sting and afflict the larvae and pupae of bees and wasps. In the southern USA *Dasymutilla occidentalis* females measure up to 30 mm and are known sensationally as 'cow-killer ants'. Generally, mutillid wasps are associated with hot, dry, sandy places in Africa, and several species attack puparia of tsetse. In Europe, *Mutilla europaea* attacks *Bombus*. In North America, *Halictus* bees combat female *Mutilla canadensis* that attempt to enter their nests to oviposit (Godfray, 1994).

The Scoliidae are a large family of big wasps, often black and sometimes banded with red or yellow. They have a slow, droning flight and a dangerous look about them. Male mutillid wasps bear a close resemblance to them. Ovipositing females burrow into the soil to find scarabaeid larvae, which they paralyse with their formidable sting. They then construct a crude cell wherein the parasitized larva is deposited. Adults are common on flowers. In Hawaii, *Scolia manilae* has been used to control *Anomala orientalis* (Scarabaeidae). Here we start to see the evolution of parental care and the social structure that characterizes higher Aculeata.

8.2.2.5(z) HYMENOPTERA; ACULEATA; Apoidea, Vespoidea. Within the bees, several groups have become parasitic on related species. They are collectively known as the cuckoo bees since they lay their eggs in the provisioned nests of other bees. In the Megachilidae, the genera *Coelioxys* and *Stelis* are parasites of other megachilid genera. In Jamaica, *Triepeolus foxi* attacks *Melissodes foxi* and *Epeolus rufoclypeus* attacks *Colletes montefragus* (Raw, 1984). In the Anthophoridae, all the Nomadinae are cuckoos. Female *Nomada* receive a chemical mimetic of *Andrena* during mating, male *Nomada* having mandibular glands evolved for this deceptive purpose (Dettner and Liepert, 1994). Within the Bombinae the sub-genus *Psithyrus* parasitizes bumble bees. *Bombus* (*P.*) *rupestris* is a close aggressive mimic of the red tailed *B. lapidarius*, while *B.* (*P.*) *vestalis* similarly affects *B. terrestris* (Alford, 1975; Goulson, 2003; Carvell *et al*., 2008). A parasitic queen spends some time in her victim's nest, thus acquiring the nest odour, and if the workers do not intercede, stings the rightful queen to death. Then she lays her eggs untroubled. Cuckoo bees do not provision, not being adapted to do so, but leave their host's workers to do the hard labour, just as avian cuckoos do. Carvell *et al*. (2008) found for the *B. terrestris*/*B.*(*P.*) *vestalis* association that, contrary to expectation, usurpation was more frequent when floral resources were abundant. Within the Euglossini, *Aglae* and *Exaerete* are cleptoparasites of *Eulaema* and *Eufriesea*. These bees confine their aggressions to egg laying. In all, the association of cuckoo bees with their hosts is extensive and specific.

In a similar way, parasitic vespoid wasps often kill the host queen, replacing her with their own. For example, the European *Pseudovespula omissa* lives with *Dolichovespula sylvestris*, while *Vespula austriaca* usurps the queenly throne of *Paravespula* *rufa*. Similarly, *Polistes (Sulcopolistes) atrimandibularis* queens drive those of *Polistes binotatus* from their nest and employ the host's workers to rear the foreign brood (Hamilton, 1996), a brood having no workers. As Hamilton (1996) puts it: 'Its made or half-made nest is obviously a valuable property to a queen bee [or wasp]', so it is unsurprising '… that usurpation has become a major evolutionary and behavioural issue with the nesting Hymenoptera.'

8.2.2.6 Non-insect predators of insects

To get a comprehensive picture of predation on insects, we consider briefly some other groups. The class Arachnida includes spiders, mites, scorpions, false scorpions and opilionids. The spider fauna of a suitable hectare may be >5 million. Spiders have preyed on insects for hundreds of millions of years. The evolution of the web for entrapment parallels that of insect flight, progressing from amorphous ground webs to the sheet webs of the Linyphiidae and to the aerial orb webs of the Araneidae. Several families of present-day spiders, however, catch insects without recourse to a web, but frequently use silk in subduing prey. For example, the Lycosidae hunt mainly on the ground, while the Salticidae jump onto their prey and overpower it. Although the tropical spider *Heteropoda venatoria* hunts cockroaches specifically, most spiders are generalists. The Thomisidae are often cryptic sit-and-wait predators who ambush insects in flowers, particularly the smaller Hymenoptera and Diptera.

Spider generations are often annual. Spiderlings emerging from egg masses, also protected by silk, often disperse by ballooning on long silken threads, like winter moth and lymantriid larvae, and hence come to be widely distributed. Indeed, aggressive interactions and frequent cannibalism among individuals on a local scale often result in a rather even spatial distribution. However, spiders still suppress the population densities of their prey, partly because they often kill far more prey than they can eat (Riechert and Lockley, 1984). In addition, females are often much more voracious than are the males. In fields, their numbers are decimated by tillage, but they are more effective predators in orchards and plantations. Even so, they are often major predators of aphids in wheat fields (Sunderland *et al.*, 1987) and of delphacid bugs in rice paddies (Settle *et al.*, 1996), restraining the pests early in the season, an example of Forrest's maxim (see Section **10.2.5.2**).

Mites, as their name suggests, are always very small and the Phytoseiidae are important for eating insect eggs. *Typhlodromus* spp. are key predators of spider mites in apple orchards (Section **13.3.3.2**). Ricinuleids are rather like ticks, but prey on insects, including termites, in the litter. Centipedes, which are in the class Chilopoda, hunt mainly on the ground in litter and in concealed situations such as within fallen wood, rather in the manner of most staphylinid beetles. In this class the Scutigeromorpha and Lithobiomorpha are mainly surface forms, but the Geophilomorpha may penetrate 50 cm down in the soil and prey upon insects there. For a brief, colourful and condensed account of all these creatures see Levi and Levi (1968).

Terrestrial vertebrates are responsible for further mortality. The frogs and toads (Anura) contain numerous species that prey mainly on insects. Many reptiles, particularly Lacertidae, Teiidae, Scincidae, the smaller Iguanidae such as *Anolis* and many chameleons are mainly insectivorous, and other small lizards will eat insects in general. They are usually common in tropical and sub-tropical regions. But by 45°N reptiles become increasingly scarce and in all temperate regions they feed only in summer.

Worldwide, birds are the major vertebrate predators of insects. Small falcons and owls and most cuckoos feed on large insects. Others like crepuscular nightjars and diurnal swifts, swallows and martins are aerial hunters. The New World tyrant flycatchers are usually sit-and-wait predators, taking a variety of medium-sized prey, either on the ground or in the air. Some families of mainly small birds, such as titmice (Paridae), Old World warblers (Sylviidae) and flycatchers (Muscicapidae), New World wood warblers (Parulidae), and cosmopolitan woodpeckers (Picidae), are highly specialized. Thrushes (Turdidae) are generalized, subsisting on berries, worms and molluscs, as well as insects. *Parus* titmice recognize not only cryptic caterpillars, but also the leaf damage they cause (Heinrich and Collins, 1983). Individual males tested had different hunting modes. While avian hunting strategies are various, birds possess extreme acuity of vision (Rothschild and Clay, 1952) using 'rapid peering' (Hinton, 1973). This acuity of these daytime hunters, evolved to improve food finding, is the likely selective force to which insects have responded by developing an enormous variety of colours and patterns (Section **10.2.3.5**). Put simply, birds have evolved better searching, finding and catching strategies and insects have become better at hiding and avoiding.

Both silviid and parulid warblers are usually highly migratory, although some species are tropical residents. Migrants exploit the dense, springtime populations of insects at higher latitudes and the increasing day length in which to catch them. Unsurprisingly, this is the time and region they choose for nesting, which exerts added pressure on exophytic insects. In the northern tropics there is a great influx of these birds in October, increasing predation on mainly arboreal insects until April. By contrast, titmice and woodpeckers do not migrate, each in their own specialized way consuming temperate insects during winter. Titmice often form bands that scour twigs and branches for overwintering insectan stages. Since their populations are typically limited by a shortage of nest sites, placing nesting boxes close to orchards in spring may well result in reduced pest insects there. But supplementary food in winter, and sheltered retreats such as hedges of *Cupressus*, assist their survival. Woodpeckers seek insect life under bark and may therefore be significant predators of many boring beetles such as those in the Buprestidae, Cerambycidae and Scolytidae (Sections **4.2.1.2(a)** to **4.2.1.2(h)**). In the Old World, the shrikes (Laniidae), like the warblers, migrate northward in spring. They prey on larger insects, impaling them on thorns as a temporary store.

In mammals there are almost 350 species of specialist insect eaters in the Insectivora: shrews, hedgehogs and moles, the last named often being a major predator of cinnabar moth (*Tyria*) pupae. Bats in the large sub-order Microchiroptera have evolved to prey on night-flying insects. They find their prey by echolocation, but many moths have devices evolved to jam this mechanism. Numerous, small dasyurid marsupials eat insects and many of these too feed at night. Most myomorph rodents (>1000 species) include insects in their diet. Several smaller carnivores, such as the sloth bear and the Fennec fox, are partly insectivorous, thus paralleling the habits of small raptorial birds, and so are other smallish carnivores in diverse families (cats, weasels, racoons). Finally, two small, disparate groups, the aardvark of Africa and the true anteaters (Myrmecophagidae) of South and Central America avidly devour ants and termites. The armadillos, which are related to and have a similar distribution to anteaters, also take various soil insects (Macdonald, 1984).

8.2.3 Insects in the control of weeds

Weeds have been called ‘plants out of place’, clearly an agriculturalist’s viewpoint. With our increasing travel between continents, opportunities for plants to travel with us also increase. As an example, in the highlands of Jamaica at the former British garrison of Newcastle, several English weed species exist, which it is said, arrived as seeds in the soil stuck to soldier’s boots. Many weeds are held in check in their native land by insects: the verity of which becomes apparent when plants are imported but these insects are left behind. Balance is often restored when such insects are also introduced. A few examples will make this clear. In Australia in 1839 a pot containing the exotic cactus *Opuntia stricta* was imported from the USA and propagated as a natural fence plant. It seemed a good idea at the time. By 1925 its progeny covered 25 million ha, some 3% of the country’s area. In that year the pyralid moth *Cactoblastis cactorum* was imported from Argentina and the lost land was gradually reclaimed. By 1940 the area affected was a mere 100,000 ha, distributed in small patches. Egg distribution (Section **10.2.5**) underlines the moth’s effectiveness. It often lays more eggs on a plant than can be sustained as larvae, hence killing the plant. But in this massive reduction the cochineal insect, *Dactylopius ceylonicus*, was involved at a later stage. Indeed, species of *Dactylopius* have been very efficient in reducing *Opuntia* stands in India, Sri Lanka, Indonesia, Madagascar and South Africa (Crawley, 1989).

Then in California, USA, the spread of St. John’s wort, *Hypericum perforatum* (Hypericacae), was halted by the chrysomelid beetle *Chrysolina quadrigemina*, introduced from the UK in the late 1940s (Huffaker and Kennett, 1969). Its larvae feed on the basal leaves during winter and defoliate the plant in spring, so causing it to have insufficient resources for reproduction. Although some million ha of grazing land were affected in 1945, only ~5000 ha remained by 1970, again mainly as isolated patches, and in shady areas. Here beetle numbers remain low, but they attack any new, unshaded fields of *Hypericum*. Also, *C. hyperici* and the gall-midge *Zeuxidiplosis giardi* have been used to limit this weed.

Musk thistle, *Carduus nutans*, which had become troublesome in Canadian pastures, has been reduced by the weevil *Rhinocyllus conicus*. An unsuccessful case there of another composite weed is *Centaurea diffusa*. While *Urophora affinis* (Tephritidae), *Sphenoptera jugoslavica* (Buprestidae) and a variety of other insects have been tried, no measurable decrease in density has been achieved (Muller *et al*., 1989). Similarly, *Tyria jacobaeae* (Arctiidae), despite often destroying >90% of ragwort seeds in pastures, nevertheless fails to control it. The plant's density appears not to be limited by the numbers of its seeds. *Lantana camara* (Verbenaceae) has become an unwanted weed in many tropical countries and a battery of insects has been used to limit it. The most successful have been *Teleonemia scrupulosa* (Tingidae), *Uroplata girardi* (Chrysomelidae) and *Hypena strigata* (Noctuidae). In South Africa the pteromalid wasp, *Trichilogaster*, has been used against the shrub *Acacia longifolia*, but unfortunately has expanded its range to non-target acacias. Bruchid beetles attack many such trees and related legumes (Southgate, 1979).

Several of these weeds spread in arid pasture. By contrast the water hyacinth, *Eichhornia crassipes*, has become a pantropical nuisance in reservoirs and waterways. Some control, especially in East Africa and Papua New Guinea, has been achieved using the weevils *Neochetina eichhorniae* and *N. bruchi* that eat the young leaves. Nutrient levels, mainly of N, P, and K, influence growth in this plant and in turn the numbers of these weevils (Raghu *et al*., 2013). But applying foliar herbicides disrupts biocontrol tactics (Wilson *et al*., 2006). *Sameodes albiguttalus* (Pyralidae) and *Eccritotarsus catarinensis* (Miridae) (Coetzee *et al*., 2007) have also been used, but many slow tropical rivers remain choked by this coarse weed. *Salvinia molesta*, another floating weed that blocks tropical waterways, has been studied in Australia (Room *et al*., 1989). The weevil *Cyrtobagous salviniae* and *Samea multiplicalis* (Pyralidae) from Brazil also thrive in nutrient-rich conditions, but only the weevil limits *Salvinia* and has provided good control in Kerala (Kumar and Verghese, 2015).

Many of the successful cases of biocontrol of weeds have been by chrysomelid and curculionid beetles. Ideally, the insect should weaken the plant so that it fails to reproduce, but it is often found that great reductions in seed output fail to achieve control. However, the weevil *Apion ulicis*, introduced into New Zealand to limit gorse, *Ulex europaeus*, frequently destroys 90% of the seeds. But gorse has a large and persistent seed bank and, like ragwort, is not limited in this way. Nor does the weevil affect the growth of these bushes (Hill, 1983).

But as in the biocontrol of insects, there may be unwanted consequences on native floras, with rare plants being especially at risk. Introduced species migrate far from agricultural habitats and adapt to new food plants (Louda *et al*., 2003). For example, *Rhinocyllus conicus* (above) was found to develop in the heads of 17 Californian *Cirsium* species (C.E. Turner *et al*., 1987). In Nebraska, USA, it caused a marked decline in the density of the Platte thistle, *C. canescens*, while there is evidence of further indirect ecological effects (Wajnberg *et al*., 2001); naturally, scarce insects dependent on such plants become extinct.

8.2.4 Insects as decomposers and soil formers

Soil is derived from inputs from above, especially roots and leaves, and from weathered rocks below, so forming a thin veneer to the terrestrial land mass (White, 2006). Here, almost all organisms ultimately return to the soil. Apart from some microbes, soil organisms depend for their nutritional and energetic needs on those living above. Only ~1–2% of the Sun's energy falling on a biotope is trapped by plants and converted into gross primary production, the rest being reflected (Odum, 1971; Section **2.2.2**) or lost in respiration. Most of this trapped energy returns to the soil when plants die and is the origin of the greater part of that used by decomposers. But living plants also donate appreciable amounts of sugars, amino acids and other organic compounds to the soil, stimulating rhizospheric interactions (Stanton, 1988; Nguyen, 2003). A smaller amount of vegetation is eaten by herbivores above ground and returned to the soil as animal products such as faeces and carcasses (Mattson and Addy, 1975; Crawley, 1997; Polis, 1999; Section **10.2.2.5**). Soils contain the bulk of the world's land surface organic carbon, and their formation is one of the most important ecological functions in which insects assist, as they comprise much of the mesofauna.

At inception, two primary, *major trophic pathways* exist underground and arise from plants: herbivory of roots and decomposition of dead plant material (Stanton, 1988). Sometimes all organisms involved are lumped together as 'decomposers'. This is very vague in so large an industry. But some *Tipula* spp., wireworms and scarabaeid beetles (see **Chapter 3**) occupy both niches and hence may be pests. Root-feeding weevil larvae such as *Phyllobius*, *Polydrusus* and *Barypeithes* reach densities of 1000/m^2 in

North American hardwood forests (Coyle *et al.*, 2011). The size of this 'decomposer' industry, measured as energy transfer, is far greater than that above ground: tenfold greater might be an average (Odum, 1971). This is because aboveground herbivores consume only a small proportion of the primary production (Polis, 1999; Section **2.4**). Two *minor pathways* exist: cadavers and faeces of vertebrate and invertebrate origin.

Although, following Charles Darwin's book, earthworms are famous primary decomposers, the living biomass of such soil insects and other arthropods may be typically 30–100 kg/ha, being greatest in rich forest soils, but overall the variation is wider than these limits. Apart from sub-soil herbivores on living tissue, arthropods include both primary and secondary decomposers. The first group, in which insects are prominent, ingest mainly dead plant tissue and pass it out as faecal pellets. Hence, they increase the surface area of this material and so make it more readily available to fungi and bacteria, which are the main decomposers farther down the biotic chain. Experiments show that when primary insect decomposers are excluded, the breakdown of dead leaf material is slow. Apart from their role as soil formers, in a wider context these arthropods cycle carbon, nitrogen and phosphorus in the biosphere (Odum, 1971). Nitrogen-fixing organisms are either free-living (Reed *et al.*, 2011) or symbiotic. Since the former generally live on surfaces the fragmentation of litter leads to their increasing numbers. Also, a great deal of dissolved organic matter containing carbohydrates and carboxylic acids as well as combined nitrogen and phosphorus, leak out of the detritus (Polis and Strong, 1996).

Temperate soils have a range of insects in this primary role. Cicada nymphs are found in warmer regions and tropical soils are rich in ants and termites (Stanton, 1988). Both Neotropical attine ants and Macrotermitinae employ fungi to degrade plant material, leading to soil formation. In selva, termite biomass may exceed 500 kg/ha, greater than that of all other animals combined. In temperate regions dipteran, coleopteran and a few moth larvae (cutworms, swift moths) are common. Generalized feeders (wireworms, leatherjackets; Section **3.2.1**), consume dead plant material when the soil is moist, but may turn to living plant roots in drought (above). Since most juvenile decomposers die before becoming adult, their dead bodies return to the soil, so forming another pathway (below). Apart from insects, fungi invade plant material and mycorrhizal associations are commonplace. These, and associations with many bacteria, are symbiotic. Secondary decomposers consume the faecal pellets of the primary ones together with their microbial contents. Essentially, they are coprophages ecologically distinct from those of vertebrate faeces. They include pre-eminently Collembola, whose densities may reach 10 million/ha, and some other Apterygota. Soil mites, especially the Oribatei, also play a role here and exist in vast numbers, as do many nematodes and enchytraeid worms. Protista, algae and bacteria are important too, some of the latter fixing atmospheric nitrogen. While invertebrate consumers of invertebrate products are widespread, those of vertebrate products are patchy. The distinction arises since vertebrates have greater body size and consequently lower population density.

In temperate regions, falling leaves and other soft plant material dying in autumn woodlands amounts to ~4000 kg/ha (Bray and Gorham, 1964) and is partly consumed by insects in the litter at this time. These detritivores slowly continue this role during the winter unless temperatures are severe. Remaining material is eaten rapidly in spring. In the tropics leaf fall is generally greater, amounting to as much as 13,000 kg/ha/a in rain forest and occurs steadily throughout the year, although some trees shed their leaves if there is a dry season (Section **2.2.3.2**). But there is no spectacular autumnal build-up of litter and soil formation is a more rapid and continuous process than in temperate regions, an effect promoted by moisture and higher temperature.

Biochemically, soil formation by physical and biotic agents involves different types of *humus* production. This is of key importance in soil fertility, as the various types retain water and nutrients. Essentially, invariant properties of soil modulate the variable inputs of water (see Fig. 10.1). We will call all dead material derived directly from plants, *phytodetritus* (Section **10.2.3.8**). Much of this erstwhile 'green mantle' passes through insects and other organisms before becoming humus. Two types of humus are formed from it: *tannin humus* and *lignin humus*. They are not definitive compounds, but groups of heterogeneous structure (Pearson, personal communication). Nitrogen-containing tannin humus comes from the leafy bulk of all plant material in which plant proteins react with dissolved tannins, also of plant origin, within or outside plant residues. So it is *generally distributed and produced regularly*. Lignified tissue in dead trees, branches and twigs forms a parallel pathway leading to dark, lignin humus characteristic of forests, and is *usually more patchy and produced intermittently*. Mainly within forests, dead trees, with their great bulk, are foci of complex insect diversity (Hamilton, 1978). If trees die standing, they shed progressively larger twigs and branches around them. If they fall and then die the pattern of lignified tissue deposited is more elongated, mirroring the tree's shape. Compared to grassland soils we can visualize the greater heterogeneity of forest soils. In the tropics, termites play a key role, although generally larval borers in dead wood in a range of endopterygote orders, including *Sirex* and *Tremex* (Symphyta), *Cossus* and *Zeuzera* (Lepidoptera), and some *Tipula* and *Dictenidia* (Diptera), belong here. Of course, a huge variety of wood-boring coleopteran larvae and adults exists. Fundamentally, diversity above leads to diversity below.

Insect activity in wood, whether living or dead, leads to rapid invasion by fungi, especially Basidiomycetes and bacteria. Living wood may be consumed by various beetles, especially Scolytidae and Cerambycidae. Indeed, the former group may bring about the death of a tree, often when it has been defoliated by caterpillars or weakened by drought or fire. A disastrous case of this is the almost total destruction of mature elm trees in Western Europe and later in North America by *Scolytus scolytus* (Section **4.2.1.2(h)**). The key point for soil formation is that insects cannot digest lignin, which is a complex of related compounds, even with the aid of symbiotic microbes (Martin, 1987). Their faeces therefore concentrate it and confine it in finely divided crumbs; a condensation process involving quinone and phenolic groups then forms nitrogen-free lignin humus.

The decomposition of mammalian, avian and other vertebrate carcasses, dead snails, worms and indeed dead arthropods themselves, which we will call *zoodetritus*, comprises a third pathway leading to the formation of nitrogenous *melanin humus*. This results from an interaction between aromatic fission products (tyrosine and tryptophan), and oxidizing enzymes produced by the soil biota. While vertebrate scavengers eat much of this material and so is redistributed and returned to the soil as faeces (*coprodetritus*), the remainder is attacked by arthropods, either silphid and dermestid beetles, calliphorid and muscid flies, or by mites. A pair of *Nicrophorus* (= *Necrophorus*) (Silphidae) beetles can bury a rat-sized rodent in a few hours (Scott, 1998) unless a vertebrate scavenger intercedes (Putnam, 1977; Section **8.3.1**). Vertebrate coprodetritus, which is rich in dissolved organic matter, is also removed rapidly by insect activity. A sequence of species typically colonizes this medium, often starting with Diptera (Borboridae, Cordyluridae and the muscid genera *Musca*, *Orthellia* and *Mesembrina*, and many others) and ending with Coleoptera. Dung beetles bury their dung balls quickly, making them unavailable to Diptera, an action increasing the depth of fertile soil. Recently, some African dung beetles were introduced into Australia to reduce the build-up of dung in cattle pastures. But herbivorous insects also produce faecal material; in particular caterpillars in temperate forest canopies produce a steady rain of it in summer. The annual value of this global service is estimated at ~$1.6 billion (Reynolds, 2012b).

A general point arises from the study of soil formation. There is a tendency for less nutritive material (phytodetritus) to be abundant and widely distributed, while more nutritive material, largely of vertebrate origin (zoo- and copro-detritus), is localized. The latter is naturally more likely to be the object of competition. In summary, the soil beneath your feet, apart from eroded bedrock, is a historical record of the death and destruction of a standing flora and a more mobile fauna.

8.3 Insects (Excluding Harmful Ones) and People

8.3.1 Forensic entomology

If a person dies or is murdered and the corpse remains undiscovered for some time, the initial police procedure is to estimate the time of death. In the short term, investigators can take the corpse's T_b and note the presence or absence of rigour mortis. But blow flies oviposit rapidly on an exposed body when the ambient temperature (T_a) is not too low and this too may be used. It is assumed that they oviposit shortly after demise, so the state of development of the largest larvae gives an estimated time of death. Since temperature is the pertinent factor, using day degrees (D^o, q.v., Section **10.2.2.2**) provides greater accuracy. In the longer term the identity of insects and other arthropods that feed on the corpse provides a further clue of the time of death (Gennard, 2007). Of course, their succession is a special case of the general one of soil production from vertebrate carcasses discussed in Section **8.2.4**.

Megnin (1894), following Yovanovitch (1888), made a systematic treatment of this subject and suggested the use of forensic entomology. Megnin had earlier studied the fauna of tombs. While there are several waves of colonization of a corpse by characteristic arthropod faunas, the main imperatives determining the succession are location, whether the body has been buried, left exposed on the ground or has drowned. Humidity, as well as temperature, influences the sequence and the presence of poisons in the corpse has an effect. Criminal activities such as burning a vehicle with the body inside also modify it (Catts and Goff, 1992).

The nature of the colonizing fauna of exposed corpses in Western Europe (Smith, K.V.G, 1973, 1986) is summarized here. Initially, a series of calypterate flies begins to breed. Before the body smells foul, species of *Calliphora*, *Musca* and *Muscina* start to consume it. In the second phase it develops an appalling stench and may be invaded by several species of *Sarcophaga*, *Lucilia*, *Cynomyia* and *Chrysomya* (Section **7.4.2.2**). These phases occupy, according to T_a, 6–12 weeks. Then the body fats become rancid and dermestid beetles and the pyralid moth *Aglossa* invade. During the period of up to a year after death there is a fourth wave of dermestid beetles, piophilid, drosophilid, sepsid and spherocerid flies, followed after a year by a fifth wave of the muscid fly *Ophyra*, and a complex of silphid and histerid beetles. Then there is a phase dominated by mites, and the remains become completely dry. A seventh wave of dermestid beetles and larval tineid moths is followed after 3 years by a final phase of ptinid and tenebrionid beetles. Predators and parasitoids will also be present.

In North America, the sequence is roughly the same at the familial level although many species are different (Rodriguez and Bass, 1983; Catts and Goff, 1992). In South Africa, Williams and Villet (2006) have reviewed work there. Clearly, a good knowledge of entomology is an essential for the forensic scientist. More recently, DNA-based methods have been used, especially as an aid to identify immature forms (Wells and Stevens, 2008, who cite 136 references). Thus, larvae of *Calliphora vomitoria* can be distinguished from those of *C. vicina* (Ames *et al*., 2006). Then the presence or absence of maggots, in relation to the state of decay of the body, may show if it has been moved to a new location after death (Nigam *et al*., 2010). An addition to the long arm of the law is *palynology*, the study of pollen. Pollen grains are highly specific, durable and of course present (except in the soil) for often brief periods of flowering. Also, plants producing them are localized. So they provide additional spatio-temporal data on the corpse, again perhaps revealing that it has been moved.

More pleasant extensions of forensic entomology have been used in archaeology. The presence of identifiable beetle elytra that attack stored grain (Section **6.3.1.2**) can confirm the original existence of a grain store, which is, of course, a milestone in the development of human culture. The vertical sequence of beetle elytra in peat bogs may be used as a time scale reaching far into the past (Coope, 1979). In archaeological sites close to such bogs, any elytra found in association with human habitation may be used to place the site on that time scale. Osbourne (1969) was able to infer, by reference to a collection of beetle parts made from the bottom of a late Bronze Age shaft in Wiltshire, that the climate there some 3330 years ago was similar to the one today.

8.3.2 Insect products

These do not constitute the formidable array produced by mammals, for example mammalian meat, leather and dairy products have no commercial equivalent in insects, although worldwide production of honey and wax from bees runs into several billion US dollar. Insect silks are exocrine secretions of the labial glands of mainly bombycoid moth larvae used to build their protective cocoons. Silks are worth a mere US$1.6 billion annually, although in antiquity the silk trade was proportionately greater than today. They are obtained from the cocoons of several species that have very large silk glands. For example, in *Bombyx mori* (Bombycidae) they are four times the length of the body and have complex folding. A cocoon may comprise a fibre ~1000 m long, several of which are spun together in commercial use. All commercial silks must be capable of being reeled. Silk production was an Oriental development. Hsi Ling-Shi, Empress of Hwang-Te, is credited with its discovery in 2640 BC (Feltwell, 1990), when a cocoon dropped inadvertently into the imperial tea and was found to unravel. The loom was developed in 2602 BC. Successive dynasties forbade export of moth and technology on pain of death. But the Japanese got the eggs in the fourth century AD and in 552 AD, in the reign of Justinian 1, two Persian monks returned to Constantinople with some *Bombyx* eggs concealed in a hollow staff and the technology in their heads (but see below). These were heady times as plague, malaria and Goths were busy ravaging the Roman Empire.

Several moths in the related family Saturniidae also produce silk: *Antheraea yamamai*, the Japanese oak silkworm introduced into Europe in 1861, produces Tussah or Tussor silk. *Antheraea pernyi* yields buff Shantung silk. In India, *A. paphia* spins brown Tasar silk (presumably a modification of 'Tussah') and *A. assama* Muga silk. The related genus *Philosamia* produces Eri or Evi silk, but this cannot be reeled. It is just possible that one of these species was the origin of silk produced on the island of Khios, before the Chinese import. According to Aristotle, Alexander the Great (356–322 BC) discovered silk production when his army over-ran Persia. Subsequently, a few Greek islands (Kos, Scio and Morea) became centres of silk production. But in Madagascar, up to 50 tonnes of 'wild silk' are collected from *Borocera cajani* (Lasiocampidae) every year. The product is reeled, dyed and woven in a small local industry (Cranston, 2016).

Bombyx mori exists only as domestic stock, probably having wild ancestry in *B. mandarina*. It has many strains, over 400 described mutant genes and is reared in several countries far from the Orient, particularly France, Italy and Spain. Silk cannot be cheap because 6000 cocoons are needed to produce one kilogram of it. In producing beautiful, hard wearing silk carpets in Kashmir only female cocoons are used as the fibres are thicker, even so, several fibres are spun together to produce the thread.

Honey, largely from *Apis mellifera*, but also from a few other *Apis* species and halictine bees, was the main sweetener until a few hundred years ago, but with the advent of sugar tends to be regarded today as a minor, if tasty, commercial product. It is the traditional sweetener in the classic recipe from the Dordogne of *canard diodene*. And there is evidence that unrefined honey especially is an excellent health food and may promote longevity (Hill, 1997), or what is more important, good health in the mature years of one's life. Honey has been traditionally fermented to produce wine (mead in England, tej in Ethiopia) and while its long-term effects may be doubtful its short-term effects are not. In Australia, apiculture is a thriving, highly productive industry (van Emden and Service, 2004), and annual yields of eucalyptus honey per hive may be as high as 100 kg. Bees wax is still valuable commercially and is used by Nepalese craftsmen in the traditional production of their bronze artwork. Propolis is a mixture of resins that the bees collect from trees and buds, and use to waterproof and seal the hive. It also has antibiotic properties. However, in many regions apiculture is under threat from agricultural intensification (Kremen *et al.*, 2002; Goulson, 2003).

There are products from scale insects, although these are often replaced by synthetic alternatives. Cochineal, also known as carmine, is extracted from *Dactylopius coccus*, a scale that feeds on *Opuntia* cacti in dry regions from Mexico to Peru, and also Jamaica. It is most usefully a food dye. Shellac, which is used in French polish, comes from *Laccifer lacca* in India. Candle wax, from *Ericerus pela*, is of rather less importance.

8.3.3 Insects as human food

While the Crustacea, another class in the Arthropoda, provides many culinary delights (lobster thermidor, crab Newburg and shrimp Creole, to name a mouth-watering few), despite their vast numbers, insects have not been able to command the attention of any reputable gastronome. We read that Indigenous Australian people prize wichetty grubs, variously classified as Hepialidae, Cossidae or Scarabaeidae, that Indigenous Americans feast on fried abdomens of *Atta* queens (not bad!) and the eggs of corixid bugs (*Artocorixa* spp.). Also, that longicorn larvae are prescribed for under-nourished children in old Japan. In the sub-Sahara, locusts, big orange caterpillars and edible stink bugs are a tasty treat. In Benin, ground crickets are roasted on sticks. But these delights do not travel well, failing to gain even a page in any reputable cookbook. Herodotus records sun-dried, powdered locusts being consumed with milk, and St Mark reports (1 Mark: 6) their having succoured John the Baptist in the wilderness. In Uganda the swarming grasshopper, *Homorocoryphus nitidulus*, is eaten either raw or cooked, and the migratory *Ruspolia baileyi* (Tettigoniidae, 'nsenene') is an object of trade. Gryllid crickets (*Brachytrupes portentosus* and *B. membranaceus*) are eaten in many parts of South-East Asia. Today in Bangkok, Thailand, street vendors sell fried locust nymphs (*Patanga succinata*) to curious tourists, but on a recent visit I was not persuaded to try them, having an entomologist's vision of the contents of their hindguts. Locust-eating marathons are held in Thailand, with the winner of a recent event consuming a kilogram in 5 minutes! The Thais, having reeled the silk from *Bombyx* cocoons, savour the fried pupae, but I found them uninteresting. Other delights are giant water bugs and dytiscid beetles (**Fig. 8.18**). Ants, eaten with onions and hot peppers, look especially revolting. But travelling through the desert on foot, one might well be surprised, delighted and relieved to find a tasty product of the eriococcid mealybug *Trabutina mannipara*. It is formed by evaporation of the honeydew, rich in sugar (mannose) and protein, otherwise known as manna.

8.3.4 Insects in science and medicine

Since many of the natural processes that occur in animals (and even plants) are rather conservative, it is frequently convenient to study them in insects. Close parallels exist in physiology, genetics and behaviour, for example. Convenience of study occurs because there are numerous species that may easily be obtained, reared and handled. They also have the distinct merit of a short life cycle, which speeds up the study of trans-generational processes, such as those in genetics, evolution, and population dynamics.

We noted in Section **13.1** that T.H. Morgan used the fruit fly *Drosophila* to verify Mendel's original genetic work on plants. His choice was so brilliant that within a few years our knowledge of animal genetics far outstripped that of plant genetics. Lepidoptera were used by E.B. Ford in both laboratory and field studies in genetics and evolution. Indeed, work by Ford (1955, 1975) and Kettlewell (1973) on industrial melanism in *Biston betularia* showed the potentially enormous power of natural selection. The Russian émigré Dobzhansky developed similar studies in the USA using *Drosophila* species. More recently, the late and much lamented genius W.D. Hamilton drew heavily on insect examples in extending Fisher's sex-ratio theory (Hamilton, 1967), in investigating altruism (Hamilton, 1972) and the nature of plant defence against herbivores (Moran and Hamilton, 1980).

The development of physiology has been aided by work on insects, particularly that of the Cambridge School initiated by Sir Vincent Wigglesworth. Indeed, the elegance of Wigglesworth's experimental methods in the 1930s, for example, those on osmo-regulation in dipteran larvae, set new standards for future work. While the circulation, respiration, digestion, excretion, osmo-regulation and endocrine control in insects show many unique features, in general these add to the comprehensiveness of general physiology. Moreover, several of these areas are directly applicable to methods of insect population control.

Fig. 8.18. Edible insects for sale in a Bangkok street. Source: Wikimedia Commons, credit to Takoradee.

Thus, studies on the physiology of insect cuticle led to improvements in the penetration of contact insecticides.

Early work on insect behaviour was accomplished over many years by the French naturalist Jean Henri Fabre, whose studies on the behaviour of bees and wasps was taken up by an international crew: Tinbergen, Evans, Michener, Malashev and Iwata. Now we know much about their behaviour; especially its evolutionary aspects. This knowledge is an effective weapon in our ongoing fight against insectan pests.

Early medicine frequently used the aid of invertebrate animals. The use of leaches is well known, that of blow fly maggots less so. Army surgeons from the Napoleonic wars to the WWI noted that wounds that had become infested with maggots healed better than uninfested ones. Similarly, during the American civil war J.F. Zacharias reported the use of maggots to clean wounds, and in WWI, W.S. Baer used them regularly. This led to more controlled applications, on cases that had not responded to regular treatment, at the John Hopkins School of Medicine in Maryland, USA. Finally, with the relentless evolution of antibiotic-resistant pathogens, there has been a resurgence of their use on chronic wounds in Europe, Israel and California, USA. Blow fly maggots produce a variety of antimicrobial peptides (AMPs) (Erdmann, 1987), for example, groups called defensins and diptericin. An AMP named lucifensin has recently been isolated from *Lucilia sericata* (Nigam *et al.*, 2010). Maggot therapy shows promise in treating foot gangrene in diabetic patients and diseases such as osteomyelitis. Cantharidin, from blister beetles, and bee venom have also been used medically.

In addition, the educational value of using insects is considerable. At the primary level their strange and fascinating ways, for example the metamorphosis of butterflies, may well stimulate a child's interest to greater development later on, while their diversity and ease of handling make them useful in more advanced biological education (Kalmus, 1960; Borror *et al.*, 1989).

8.3.5 Aesthetic value

The true aesthetic value of insects can be appreciated fully only by the fortunate few schooled in entomology. To stand in the early light in a Neotropical forest by a flowering *Gongora* orchid and watch the arrival and departure of large, metallic-green euglossine bees, is among the greatest wonders of nature (Dressler, 1982; Cameron, 2004). But it is all the more fulfilling if you know that such bees are males who travel perhaps 100 km a day, at speeds of 50 km/h, to locate many such orchids. That they use the plant's aromatic products to woo mates, that their flight muscles have the highest metabolic rate of any known tissue (Casey *et al.*, 1985) and that their metallic colour is part of a mechanism of thermal control (Willmer, 1983). Otherwise they are just a pretty flash of colour. As Niko Tinbergen once put it, '… beauty increases with increasing awareness of detail.'

In the same setting, metallic-blue morpho butterflies form a splendid contrast to the lush background. To have seen the impossibly large swallowtail butterfly, *Papilio homerus*, drifting down a leafy Jamaican mountain valley (Garraway *et al.*, 2008), or the big hawk moth, *Manduca sexta,* feeding at waxy-white cactus flowers in the moonlight (you can hear the whirr of its wings), while ephemeral, are superior experiences to owning a tin tray stuck with butterfly wings. Those interested in the aesthetics of nature should see Brady (2003). The insect collections one makes are evocative of the situations in which the beasts were caught and to be regarded as finer aesthetically than any bought-in collection of exotic butterflies. Even so, designs based on insects are often used on jewellery, fabrics and various other articles. The excellence of the design depends not only on the worth of the artist, but also on their knowledge of insect anatomy, which is often extremely fragmentary.

9 The Principles of Insect Autecology 1: Some Key Concepts

9.1 The Types of Ecology, Life-History Strategy and Genetic Influences

Ecology falls into two complimentary sections: *community ecology* (synecology) and *single-species ecology* (autecology). Synecology, like much biology, has a history of ~160 years and concerns the relationships, numerical or otherwise, of organisms in biological communities. Animals and plants are given relatively equal consideration. It also covers the operation of those topographical and climatic factors determining the global distribution and composition of such associations (*biomes*) (Section **2.2.3**). Synecology concerns biotic systems. Indeed, the relationships of producer and consumer organisms in the *pyramid of numbers* (q.v.; Section **9.8**), and the energy, nutrients and important elements such as carbon, nitrogen, phosphorus, calcium and iron they cycle, constitute *ecosystems ecology* (Holling, 1992), which probably arose from studies of natural, isolated plant communities.

Autecology has developed over the last 60 years (McIntosh, 1995), and is rooted in individual, single species and the species concept (Haeckel, 1866; Mayr, 1963; Paterson, 1980; Mallet, 1995; Templeton, 2001; Sections **9.6** and **9.10**). It is more specialized than synecology. We consider it here for insects only, especially pests. *There is always a single 'focal' species* (Turchin, 2003), in relation to which *environmental components* are considered. While these are the same as in biotopes, only those relevant to our species, especially when they affect its reproductive success (RS), are of interest. Indeed, *synecology* is at root an integration of the *autecology* of all the species, both plant and animal, existing at a locality. Physicochemical factors aside, consider a *tritrophic interaction* between a plant, a phytophagous moth and a parasitoid. If the moth is our focal species, the plant is *larval food* and the parasitoid an *enemy*. Both may affect the moth negatively, reducing its RS. But if the parasitoid is our focus the larval moth is food, and if the larva kills it by encapsulation as is often the case, its food has terminated its survival. The status of these biotic factors changes with the trophic level of the focal species. These are *direct actions*. But the plant may not be a passive party (Section **2.4.2**), and if the moth's larva uses the plant's defensive chemicals to kill the parasitoid, there is an *indirect action* (Thompson, 1929; Sections **9.8** and **10.1**).

The theories of animal numbers by W.R. Thompson and A.J. Nicholson initiated ~1930, while somewhat historical now, are nevertheless central to autecology (Section **11.2.2**), just as are the pre-Fisherian studies of evolution by Darwin, Wallace and Spencer. Autecology itself was given a basic foundation when in 1954 two Australian ecologists, H.G. Andrewartha and L.C. Birch (Fig. 9.1), wrote the seminal *The Distribution and Abundance of Animals*. Their work is full of interesting examples and ideas. We find the recently popular metapopulation dynamics, relative shortages, spatial refuges and range limits all treated extensively. The '*Distribution and Abundance*' is to autecology what '*The Origin*' is to evolution. It is doubly relevant for us because of its many insect examples, and because its title links distribution and abundance as the two basic aspects of insect populations. *Distribution* relates to the arrangement of individuals on several spatial scales (Levin, 1992) on the Earth's surface (Section **9.2**), and of *abundance* we will speak shortly.

Autecology is essential for studying pest insects in general and their populations in particular (Berryman, 1999). It takes place against the backdrop of synecology, the natural basis to investigate agroecosystems (Section **13.1.1**). Several aspects of *habitat* affect focal individuals. Therefore species living lower in the food chain than the focal one *aggregate its resources*, so affecting its distribution. *Macroecology* is a recent move to draw wide-scale patterns from community structure (Brown and Maurer, 1989; Gaston, 1998; Gaston and Blackburn, 2000).

Fig. 9.1. L.C. Birch, who with H.G. Andrewartha, was a prime mover in the development of autecology. Unfortunately an adequate photograph of H.G. Andrewartha was not available. Source: Wikimedia Commons.

We find that species with wide regional distributions tend to have high local population densities (Section **12.3.4.1**), which impinges on autecology. Such 'first-order' patterns must be extracted before finer details can be analysed (Lawton, 1999). Ecology is hierarchical but needs structural development (Walter, 2003), which I provide here for insect autecology. But a lack of dialogue between its various branches exists (Levin, 1992), a perennial failing in any human endeavour.

Insect autecology, while having the same basic pattern as that for other terrestrial animals, has special features. Insect achieved fecundity (AF) ranges greatly, from unity in sexual pemphigine aphids to >10,000 in a few groups that scatter eggs, especially eucharitid parasitoids. It is a major part of life-history strategy (LHS). Indeed, *egg distribution*, a further part of LHS, initiates the distribution of successive generations. It too varies widely from liberal scattering, to single batches of >100 eggs, to deposition in ones and twos on isolated food plants or on/in host insects. Such extensive egg distribution on specific resources (Section **10.2.5.2**), quite unlike that of other terrestrial invertebrates, shows the evolved ability of some insects to exploit the three-dimensional nature of their environment. Some structurally and behaviourally advanced insects (q.v.) can therefore find widely scattered resources speedily (Section **10.2.4.1**). Other insects move only a little, as do flightless *Scapteriscus* (Section **3.2.1.1(a)**) and gypsy moths, or are vagrants, like aphids. Again, juvenile mortality varies greatly, from <25% in some wasps with parental care to >95% in most insects on plants (Cornell and Hawkins, 1995). Students note: *mortality and survival* are reciprocal terms and an individual's death may have an extrinsic or an intrinsic cause (Section **9.6**), the latter, the 'constitutional weakness' of Thompson and Parker (1928a), is often due to genetic defects acting during development. But when ecologists use 'mortality', they usually imply an external cause. To be clear, in genetics there is a *genetic environment*, that is the result of the entire genome, a *physiological environment* within the organism, and an *external environment* outside it. But the key feature in insects is that, largely through increasing adult mobility through flight, the dynamics of adults becomes *progressively uncoupled from that of their juveniles*. Although this is least when reproducing adults forsake their mobility, as in pest aphids, grain beetles and lice, it can be extreme in highly developed individual searching capacity HISC species (Section **10.2.4.1**) such as dragonflies and hawk moths.

The comparative ecology of a group of animals that are related in some way, either taxonomically or because they are guild members, is an extension of autecology (Root, 1973; Hawkins and MacMahon, 1989; Gittleman and Luh, 1992). Since the former groups arose from a common stock their comparative ecology and population dynamics (Williams, 1947; Price *et al.*, 1998) may possibly reflect phases in this evolution (Section **12.4**). Comparison is a powerful intellectual tool (Bradshaw, 1987; Section **2.1**) especially in ecological and evolutionary studies, revealing insights that otherwise would remain obscure. Examples are comparisons of resistance to freezing and drying power of the larval environment of *Tipula* spp., while the large size of the mandibles in *T. paludosa*, relative to those of most other *Tipula* spp., is an explanation of its pest status (Freeman, 1967b; Sections **10.2.3.3** to **10.2.3.4**). Heat tolerance in several species of South African blow fly maggots (Richards *et al*., 2009) provides a recent example. Note also work on three *Pieris* butterflies in relation to their common parasitoid *Apanteles glomeratus* (Ohsaki and Sato, 1990; Section **5.2.1.4**(**h**)). For the notorious pest *Anastrepha* (Section **6.3.1.1**(**l**)), Aluja (1994) proposed comparative ecological studies to advance understanding, while comparative work on other fruit flies has aided our knowledge of speciation (Bush, 1994; Turelli and Orr, 2000; Turelli *et al*., 2001; Coyne and Orr, 2004; Section **9.10**). Such studies are essentially *comparative autecology* (Section **12.3.4.4**(**e**)).

Evolutionary ecology came to prominence fairly recently, although early ecologists knew their subject should be viewed in this context. Levin (1992) remarks: '… an evolutionary perspective is critical for understanding organisms'. Its development simply reflects a trend of increasing biological specialization. Such studies, however, have often been strangely marginalized (Antonovics, 1987), or *biased by ideology*. Variations in all innate attributes expressed in individual phenotypes and the factors influencing them (above; Section **10.1**) have ecological, population genetics (Birch, 1960; Endler and McLellan, 1988; Berryman, 2003) and *evolutionary consequences*. Thus, the *inferior genotypes* in genetics broadly translate into *reduced fertility and/or reduced survival* of individual phenotypes in autecology.

Originating in one of Fisher's seminal contributions (Section **9.7**), a major subject area here is LHS (Cole, 1954; MacArthur and Wilson, 1967; Pianka, 1972; Stearns, 1980, 1992; Roff and Emerson, 2006). MacArthur proposed that two opposite modes of selection exist, one for high reproductive output (*r*-selection) and so small size, the other for competitive ability (*K*-selection). Intermediate cases form a continuum (Table 9.1). An LHS is a *set of co-adapted traits designed by selection to address particular ecological situations*. It is often assumed such traits (e.g. body size, age at maturity, survival and fecundity) are not limited by other factors, but free to co-evolve, that is, there is an 'excessive reverence for the idea of adaptation …' (Thompson, 1929; see also Gould and Lewontin, 1979). *Evolvability*, that is, the ability to evolve (Houle, 1992; Wagner, 1996; Tautz and Schmid, 1998; Jones *et al*., 2007), is directly related to the *additive genetic variance* (V^2_w) of traits in the direction of selection (Fisher, 1930; Price, 1972; Burt, 2000; Conner, 2003). It is 'the genome's ability to produce adapted variants when acted upon by the genetic system' (Wagner and Altenberg, 1996). Genomes have the capacity to yield adaptive phenotypes. Such adaptation includes the feature of phenotypic plasticity (q.v.). However, rates of evolution and adaptive radiation are also affected by ecological opportunity (Wright, 1975). Of course, genes code not only for a given phenotypic trait; some genes act as switches or modify their action, called *epistasis* (q.v.) (Fisher, 1918; Turelli and Barton, 2006). They work intermittently in the *genetic environment* (above) (Wagner, 1996), like lights in a big office block after hours that are turned on only when needed. Most traits of interest in life-history work (e.g. body size, fecundity and age at maturity) are usually affected by several genes or loci (Lande and Shannon, 1996; Roff and Emerson, 2006). Size, for example, is not just a result of better food or a benign physical environment, but also of a superior genome. And there may be *correlational selection* producing a set of traits having but a single ecological function.

Minimally, evolution is a two-phase process: (i) the creation of new variants; and (ii) the replacement of older variants by these new ones. Clearly, phase two cannot proceed unless phase one permits. Then factors such as allometric growth

Table 9.1. A suggested *r*–*K* continuum in some dipteran genera. The insects listed vary from extreme *r*-selection at the top, to extreme *K*-selection with the opposite characteristics at the bottom.

Species	Annual generations	Fecundity	Egg size	Migration
Culex	Numerous	High	Small	Great
Simulium	Fewer	High	Small	Great
Musca	Less numerous	High	Small	Considerable
Phlebotomus	Less numerous	Lower	Small	Restricted
Mesembrina	Less numerous	Moderate	Large	Considerable
Tipula	Annual	Moderate	Small	Very limited
Glossina	Several	Low	Progeny pupal	Limited

and physiology often channel or constrain life-history evolution (Waddington, 1957; Berry, 1985; Maynard Smith *et al.*, 1985). Constraints can be due to negative genetic correlations between major fitness components (Lande, 1982). Thus, in *Colias* butterflies thermal adaptation limits the flight motor's performance (Watt, 2000), that is, a physiological restraint legislates behaviour (see Section **10.2.4.1**). Also, an advantageous gene might be linked tightly to another that has negative effects (Bradshaw, 1991; the opposite of 'hitch-hiking', q.v.) and there may be antagonistic pleiotropy (Moran, 1992a). One also assumes that *trade-offs* (Fisher, 1930; Section **9.7**) between traits maximize fitness, a concept integral with LHS, although these are not universal (Foyer *et al.*, 2007; Chapuis *et al.*, 2010). But the genomic orchestra is not in perfect tune because *genetic conflict* (Section **9.6**) is commonplace.

But there has been some confusion. Referring to a model employing pleiotropic over-dominance to explain the maintenance of genetic variation, Gillespie (1984) remarked '… high heritabilities [are] commonly observed in metric [= measurable] traits'. However, Price and Schluter (1991) suggest that since life-history traits are usually based on morphological and other metric characters, especially body size, they should have *lower heritability*, '… because they are one step farther down the causal pathway from genes to phenotype; additional random factors come into play at each step'. But again, traits related to fitness should have higher additive genetic and non-genetic variability than those under weak selection (Houle, 1992). In a review Kingsolver *et al.* (2001) state that even with metric traits strong selection is rare, while data on physiological traits are inadequate. For wing-spotting patterns (a metric trait) in the butterfly *Bicyclus anynana*, however, 25 generations of experimental selection produced all the diverse metric patterns found in the many species of this genus (Beldade *et al.*, 2002). No morphological restraint was apparent. But in a physiological example, the Australian rain forest fly *Drosophila birchii*, 30 generations of experimental selection for increased resistance to desiccation produced no response (Blows and Hoffmann, 2005). Its populations are ostensibly at an evolutionary limit. Again in contrast, in *D. melanogaster* the evolvability of resistance to desiccation is high! Also, selection for mating success (sexual selection) is stronger than that for survival (natural selection). Therefore while evolutionary change has genetic, developmental and design limits (Arnold, 1992; Houle, 1992), the situation appeared problematical (Blows and Hoffmann, 2005). Finally, Roff and Emerson (2006) after an extensive review (143 references) conclude that 'the heritability of life-history traits is generally lower than [that of] morphological traits … dominance variance contributes more to total genetic variance of the former traits than [that of] the latter', so clarifying Price and Schluter's (1991) view. Epistatic effects are common in both cases.

Evolution at this level has four stages (Watt, 2000): (i) *genotypes → phenotypes*, here molecular and developmental mechanisms interact with the external environment; (ii) *phenotypes → performance*, where alternative phenotypes express different levels of adaptedness to extant environments; (iii) *performance → fitness*, the demographic consequence of such performance integrated into absolute and then relative fitness; and (iv) *fitness → genotypes*. Here genotypic fitnesses interact with population genetics factors such as population size, inbreeding, migration (Harrison and Hastings, 1996), random genetic drift (RGD, q.v.; Fisher, 1922; Wright, 1932; Endler and McLellan, 1988, their Table 1) and mating systems, to yield the genotypic frequencies of the next generation. For (i) note that the *epigenetic system* (Wagner, 1996; q.v.) plays a key role, and for (iv) gene frequencies in a population are changed by processes in addition to natural and sexual selection. Genotypes and phenotypes are inexplicable without mutual reference (Watt, 2000), the genetic play is on an ecological stage. The fund of genetic variability stored in the gene pool, a tangible record of what has been successful in the past, promotes phenotypic diversity in the population, upon which selection then acts. Such selection produces immediate effects, but the evolutionary response depends on genetic variation, relating to Watt's phase (iv). These phases are repeated in each generation. They respond to *current* selective pressures if they are able, but this *may not lead to evolutionary advance* (Fisher, 1930; Price, 1972; Van Valen, 1973). Of course, selective pressures vary spatially as well as temporally. Between patches and more so between habitats, selection exists *as a mosaic of different forces*, thus promoting variability.

In all there is *directional selection* promoting change, and *stabilizing selection* promoting stasis. Major genetic structures coding for essential processes, such as the Krebs cycle and the Embden-Meyerhoff glycolysis, are common to most organisms, however, are necessarily conserved (Fitzpatrick *et al*., 2005; Section **1.4.4**.). Also conserved are those that code for the *bauplan*, the basic body structure (Wagner, 1996), and the *homeotic* genes that determine the identity of the body regions (Tautz and Schmid, 1998). These are *constraining processes*. Then, rather than 'evolve out of trouble' when there are long-term climatic changes, many beetles and most likely other insects 'track the shifting climatic zones' (Coope, 1979; Section **8.3.1**). Recent shifts in insect distribution (Section **12.3.4.1**) contemporary with global warming and the fact that tropical insects usually remain in the tropics add support to his view. The genetic variation that does occur is in the species-specific and population-specific gene pools. When genes are lost from marginal isolates this compromises variation and thus adaptability. But only genes *that vary* in the population can be lost; clearly, major genes or genetic structures possessed by all individuals cannot be lost. Often insufficient novel genetic change exists (Punnett, 1912; Bradshaw, 1991; Bridle *et al*., 2009) to allow evolvability, a situation occurring if all genetic variation had already been used up by selection, which may be so for *D. birchii*. Without variation there is no evolution (Maynard Smith, 1983b; Bennett, 1991), leading us to enquire how variation may be regulated (Hamilton, 1996). But some types of phenotypic mutants are more likely than others (Endler and McLellan, 1988). The clear message for the ecologist is that *genetic imperatives must always be borne in mind* (Sheppard, 1956; Sugg *et al*., 1996; Conner, 2003), especially when considering LHS, distribution and insect numbers (Section **12.3.4.4(e)**).

Classically, *r*-selected insects (aphids, mosquitoes) outstrip the effects of inimical factors by producing huge surpluses of migrant adults that seek resources elsewhere, massive losses ensuing (Taylor, 1977; Freeman and Ittyeipe, 1993; Ward *et al*., 1998). Even so, the very production of great numbers of offspring enhances population persistence (Bürger, 1999). Since short generation length is the key to rapid increase (Cole, 1954), time-dependent features such as large size, complex structure and mate choice will be compromised. *K*-selected insects tend to be larger, take longer to develop and often stay put, dealing with adverse physical and biotic factors *in situ*. Other selective modes are mooted: there is no *a priori* reason why selection should be bipolar (MacArthur, 1972). Thus, *adversity selection* might well operate under physical harshness (Greenslade, 1983; Sømme, 1989; Section **10.1.1**) and other modes may well exist, for example, on age. Also, individual searching capability (Section **10.2.4.1**) may be so viewed, but by contrast usually requires clement weather. Arctic insects suffer a harsh climate limiting flight and a short favourable season, some take years to complete a generation (Strathdee and Bale, 1998). During low temperatures in temperate regions, a few exceptional genera (e.g. *Bombus*, *Eupsilia*) employ heterothermy permitting flight, size being a factor. Others, such as little trichocerid flies and a few geometrid moths, fly with their flight muscles just above zero (Heinrich and Mommsen, 1985). While the activities of tropical insects are usually unrestrained by ambient temperature, resources may be harder to find since floral complexity there is greater (Janzen, 1970, 1981).

A further point is that there are often genetic changes with distance through the distribution of a species. In turn, the phenotypes also vary gradually, so forming a *cline* (Huxley, 1938). Clines result from the balance between gene flow and changing selection (Haldane, 1948). Some clines are of great antiquity. Fossils show that two geographical races, embracing a narrow cline, of the hydrophilid beetle *Helophorus aquaticus* have existed in Europe for >120,000 years (Angus, 1973, in Coope, 1979). Clines may occur from north to south, from wetter to drier areas, from inland to the coast, with altitude, and between polluted and natural areas. In *Chilocorus stigma* (Coccinellidae), a systematic change in karyotypes (q.v.) occurs from Alberta, Canada, to the east of the USA (Smith and Virkki, 1978, in Sloggett and Honěk, 2012). Melanic forms of the moth *Biston betularia* are frequent in industrial areas of the UK (Ford, 1975). Such adult morphs and several similar cases evolved in the nineteenth century, centring on highly polluted areas, where they were later shown by field experiments to have a cryptic function. With the advent of clean air policies melanic moths became less frequent, so reversing evolutionary change. A cline may be regarded as the *linear* expression of a selective gradient, an ostensibly simple form of the *spatio-temporal selective mosaic*. However, *in plan* irregularity of the cline is inversely related to the moth's dispersive capability: variation being greater in the weakly flying *Gonodontis bidentata* (Geometridae) than in the powerful *Triphaena pronuba* (Noctuidae) (Bishop and Cook, 1975).

Sex ratio theory (Fisher, 1930; Verner, 1965; Hamilton, 1967; Emlen, 1968; Colwell, 1981;

Section **1.5**) forms another subset of LHS, one developing recently (Hardy, 1992; Van Vugt *et al.*, 2009). There are two aspects: the *primary sex ratio* in the eggs and the *secondary sex ratio* at mating. These ratios may differ due to differential mortality of the sexes during development, but the primary ratio, in which equal investment in the two sexes is expected, is unaffected by such mortality (Leigh, 1970). Fisher first explained why such investment is equal. If either sex were in a minority it would gain an advantage in RS and hence in passing genes to posterity. This is easy to see if males were fewer than females, say a ratio of 1:2. Then average males would have twice the RS of average females. But since maleness is advantageous, any genetic system favouring it would spread until equality was achieved. Since the secondary ratio relates to the proportion of females in a population, their mating prospects and fertility, it can be a key factor in its dynamics (Freeman 1976, 1981c; Waage, 1982). But some pairs produce more males than females, and vice versa for other pairs (Verner, 1965). In the wasp *Sceliphron* (Section **8.2.2.4(n)**), small females produce two sons per daughter and vice versa for large females (Freeman, 1981c), although the overall primary sex ratio is ~1:1.

So, factors acting on growth, mortality, fertility and sex ratio affecting RS have evolutionary outcomes (Birch, 1960). Then, *natural selection* and *sexual selection* may conflict (Andersson, 1994; Zuk and Kolluru, 1998), or operate synchronously (Kirkpatrick and Ravigne, 2002), while the latter is affected by intra- and inter-sexual forces (Moore, 1996). Sexual selection should be more marked where adults are long-lived. Darwin (1871) suggested that while females retained their ancestral form under natural selection, male forms diverged under sexual selection. The latter results from females being choosy (Trivers, 1985), or from males evolving structures used in rivalry and displays. Only males of the pierid butterfly *Anthocharis cardamines* have showy, orange-tipped wings. In many tunnelling beetles elaborate horns used in conflicts between males have evolved (Emlen *et al.*, 2005). Wallace (1865) held that natural selection itself, driven by ecological forces, could cause females to diverge from the original type, and analyses by Slatkin (1980, 1984) and on world *Papilio* by Kunte (2008), support his view. This is so, for example, if females when burdened with eggs are less able to avoid predatory attacks, while other situations may be envisaged readily. One often found in moths, where resting females signal by emitting a sexual pheromone, is a case in point (Williams, 1992). Such pheromones are rarely detected by enemies, only by potential mates. Sexual selection operates on a female's ability to attract conspecific mates and the efficiency of males to locate such females. Both are often habitat specific (Paterson, 1982). Overall, when males use more energy and are exposed to increased risk during searching, they should be the more vulnerable sex (Zuk and Kolluru, 1998), as in our own species (Trivers, 1985). Apart from Andrewartha and Birch's books (1954, 1970, 1984), insect ecology texts exist by Clark *et al.* (1967), Varley *et al.* (1973), Dempster (1975), Price (1984, 1997), Price *et al.* 2011) and Speight *et al.* (1999, 2008). Below and Chapters 10 to 12 present a condensed view of our considerable knowledge.

9.2 What are the Questions in Autecology?

Andrewartha (1970) defined population ecology as the laws governing the numbers of animals in relation to the areas they inhabit. Andrewartha and Birch (1954) posed three questions for autecology, which I reframe slightly.

1. Why does our focal insect occupy so much of the Earth's surface and no more?
2. Why is it sometimes common and sometimes rare?
3. Why is it common in this place and rare in that place?

Herbert Spencer (1864; Fig. 9.2) wrote 'There is a distribution of organisms in Space, and there is a distribution of organisms in Time'. An observation that leads directly to *actual* and *potential* distribution (Section **9.5**). 'Actual' meaning what we observe at a given time, and 'potential' roughly equating with what will probably occur through several generations. So, it is nothing new if we condense these questions into the more concise: '*What causes the variation and limitation in population density of the focal species in space and time?*'. These basic dimensions thus form an *environmental template* (Southwood, 1988) against which changes in the population density of the focal species must be estimated and causes sought.

Questions 1 and 3 lead directly to spatial dynamics. Unlike question 2, they are primarily *time-independent*

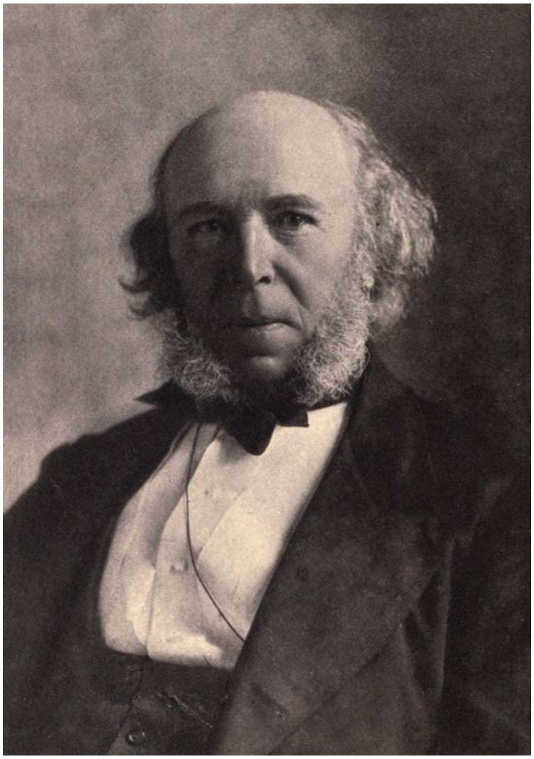


Fig. 9.2. Herbert Spencer, a prominent biologist and contemporary of Darwin in the mid-nineteenth century. He originated the term 'survival of the fittest'. Source: Wikimedia Commons.

properties of population. Question 1 has received attention recently under the term *geographical range limits* (Gaston, 1998, 2009a and b), usually without a reference to these authors! Range extension relates not only to the effects of climatic change on regional distribution (Coope, 1977, 1979), but also to the spread of introduced species, both pests and biocontrol agents, and so involves *physicochemical* and *biotic* factors. Further, a species generally comprises many populations, namely it has a *global distribution* (Section **12.3.4**) and, of course, genetic modifications may well be at work (Section **12.3.4.3**).

However, their terms 'common' and 'rare' are not the same as 'high population density' and 'low population density'; rather, they refer to how great or how small a proportion of a local resource our species consumes. This leads us to consider how 'abundance' should be measured. These terms are *relative*, not *absolute,* to resources, and hence may be explained better by *population intensity* (below). For those interested in a little history, and also for those who are not, the concepts of *absolute* and *relative* date from an ideological war between Socrates and the Sophists in Athens in the fifth century BC. Socrates promoted the concepts of absolute justice and truth, but the Sophists led by Protagoras, who in the main were lawyers anxious to retain rhetorical freedom, insisted that they were relative (Russell, 1961). So, the terms *greater* and *lesser* are relative, meaningless unless defined in relation to something else. Number, however, is the only absolute measure of population size as population density is *relative* to the area occupied and often confounded by movement (Taylor, 1984). Their terms 'common' and 'rare' are *relative* to resources, not to area. Relative measures are useful in expressing population size and in investigating competition, but when explaining numbers absolute measures are essential for reasons soon to be discussed. In an important extension, Hanski (1991) redefined commonness and rarity with respect to metapopulations (Sections **9.4** and **12.3**).

Andrewartha and Birch's three questions comprise the upper structure of autecology, namely population dynamics. Here, empirical and mathematical approaches are employed, but unfortunately may remain separate. They rest, however, on a more general foundation, the *relationship of the innate attributes of individuals to their external environment* (Section **10.1**). These attributes or components are rather heterogeneous, but for ecological purposes can be distilled into *development, survival*, *movement* and *reproduction*. *Physiology* and *behaviour* are major components (Krebs, 1972, p.10). We now consider briefly how these two disciplines relate to and affect autecology. Physiology, the study of an organism's internal processes, interests us because animals have evolved a degree of independence from the vagaries of the external environment (Thoday, 1953), encapsulated in Claude Bernard's adage 'La fixitée du milieu intérieur est la condition de la vie libre'. Ultimate examples are camels in deserts, polar bears in Arctic wastes and petrels in the oceanic vastness. Among land invertebrates, insects may show great independence from the external environment and resistance to its extremes. But physical factors mediated by physiology often play a dominant role in their ecology and hence their fitness. Such factors also act directly on behaviour, as in taxes and kineses (Section **10.2.4.3**). While the links between behaviour and autecology are complex, they always involve movement (Dawkins, 1989) and usually locomotion, which are *innate attributes*. Taylor (1986) points out that behaviour and movement are almost interchangeable; indeed, the former exists only as measurable motion in real space. Immobile organisms such as most plants, insect eggs and most pupae cannot behave, although one could regard abscission of infected fruit as plant behaviour. But this, unlike animal movement, is irreversible. Behaviour always has a cause (Eibl-Eibesfeldt, 1970), is constrained by what is physiologically possible, is often influenced by physiological state and is contingent on *recognition*. When two individuals are involved there is information transfer, both true and false. Deep down, it depends on the anatomy of the nervous system (Hildebrand, 1995; Chapman, 1999). So, as well as simple responses to external stimuli, insects have built-in *pattern generators*, often housed in the sub-oesophageal ganglion. Therefore behaviour involves mainly, but not exclusively, biotic factors. Then, small changes in behaviour can engender big changes in population dynamics (Freeman, 1981a). Ultimately, the behavioural and evolutionary imperative for individuals is to maximize their RS.

9.3 Abundance, Numbers, Population Density and the Number/Density Anomaly

Definitions are crucial in ecology: we should all try to speak the same language (Elton and Miller, 1954; Richards, 1961; Varley, personal communication, 1963; Jaksic, 1981; Berryman, 2002). Slobodkin (1986) remarks: 'On occasion, metaphors have replaced the empirical world as foci of discussions, while precise meanings and derivations have been forgotten in the process' (Section **11.5.1**). Paterson (1982) cautions: 'Words and terms should not be degraded as, … has occurred with …"niche" … The rules of scholarship require one to use the original literature….'. Where feasible the use of words in biology should be as close as possible to their meaning in general English, so that arguments may be followed without precise knowledge of definitions, desirable as this is. But with the growth of *meta-analysis*, where 'the results of [several] separate studies are put onto a common scale' (Gurevitch *et al.*, 2001), an unambiguous baseline is essential. Following Andrewartha (1970), we pay attention to the ways in which the numbers of animals are measured and how the areas they may occupy are defined. We start with the much abused term *abundance*.

Consider a one-hectare plot of cabbages (the habitat; Fig. 9.3) infested with the aphid *Brevicoryne brassicae* (Section **5.3.1.1**(**h**)) (the focal species). Say the plot contains 10,000 cabbages (patches) and 100 aphids per cabbage, making a million aphids with a population density of 100 aphids/m^2. However, if there were 20,000 identically infested cabbages in the plot there would be two million aphids and their population density would be 200/m^2. Relative to each cabbage the population density, properly '*population intensity*' (Southwood, 1978), is the same, but relative to the Earth's surface the population density is double. The density of food plants, more generally of *resource patches*, affects the (*absolute*) population density of the aphid, although the (*relative*) population intensity is unchanged. When explaining why our species is spatially dense, the quantity of its food resource, here the number of cabbages in the plot, is a major factor (see Fig. 14.6 in Andrewartha and Birch, 1954). We therefore put population density to one side and explain its variability due to environment, including quantity of food in each cabbage and in the plot, as in this example, as well as other factors such as temperature, food quality and enemies (Section **10.1**). We keep population intensity constant here, but in reality it would vary. Although in terrestrial ecology *population density* usually relates to two-dimensional space, *population intensity* usually relates to three-dimensional space, particularly that provided by plants.

There is a semantic problem in using the word '*abundant*', although it is ubiquitous in the literature. In general English the word is not synonymous with 'number' but expresses the idea of 'plenty'. *The New Shorter Oxford English Dictionary* (SOED) (Anon, 1993) defines it as 'a large quantity, plenty' and in (1980) as 'less correctly as number', and '*abundance*' as 'overflowing, more than sufficient, plenty'. So 'low abundance' is not a cute oxymoron, just confusing. Elton (1927, p. 34), defining animal ecology carefully, uses the phrase 'distribution and *numbers* of animals in nature'. But the term is often used loosely: deplorably, authors may not bother to separate 'population density' from 'number' or from 'population intensity'. Such loose use can also lead to ambiguity in conservation work (Garraway *et al.*, 2008). Hanski (1982), however, defines it as 'the number of individuals at a local population site'. Brown (1984) states: 'I shall

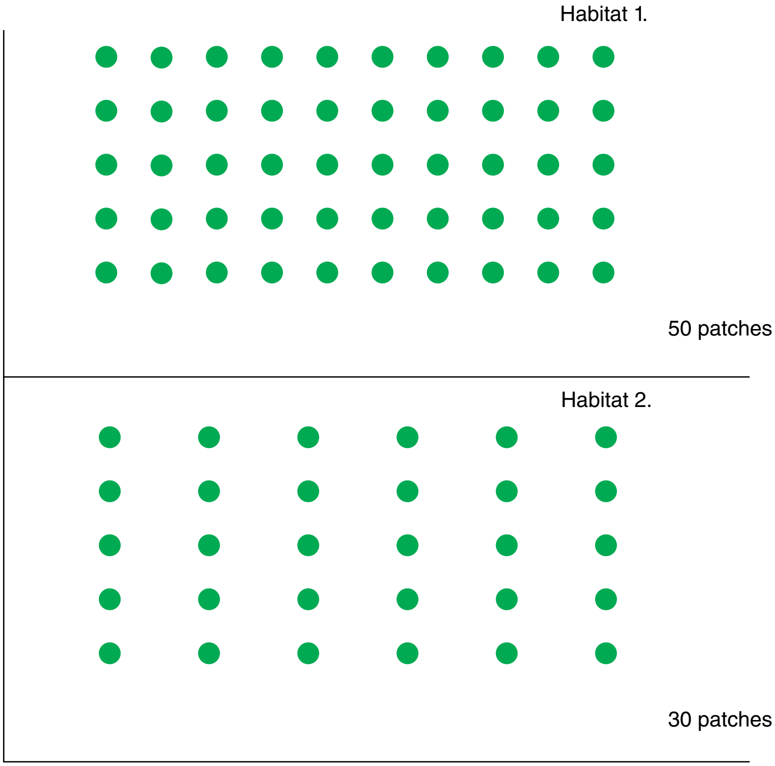


Fig. 9.3. Effect of spacing patches within a habitat. Fewer patches reduces total numbers in the habitat. But the figure illustrates only part of the story. Patches will also vary in size, spacing (non-equidistant) and suitability. See also Fig. 12. 4. The same principle applies to habitats in a landscape, an effect that is material when a given crop is grown extensively.

often use the term *abundance* to refer to local population density, ...'. But let us consider this important matter further.

Apart from distinctions between population density and population intensity, we examine the link between *numbers of individuals in a population* and the *density of that population*. Metric difficulties arise since *animals move around*. The *number of animals comprising a population does not always occupy the same area over several generations, during the life cycle, or even during the diurnal cycle*. For example, in *Tipula paludosa* (Section **3.2.1.2(f)**), the larvae inhabit moist soil under grass. Imagine a sloping pasture with a pond at the lowest point excavated to water cattle. In a wet September females lay eggs all over the pasture and surviving third larval instars have a similar distribution in spring. But suppose a drought sets in, affecting the higher parts of the field first because of natural downward drainage. Larvae would try to seek the lower, wetter parts of the field, although many would desiccate. The population concentrates near the pond, a contraction in its distribution. Now, if our sampling had been comprehensive it would show this redistribution and subsequent decrease in population number. But if it had been confined to the vicinity of the pond it would show an increase when in fact mortality had reduced numbers. Population redistribution (Section **9.5**) obscures mortality, producing the paradoxical effect of increasing density but no reproduction.

Movement confounds density and distribution (Taylor, 1984). While density and numbers in a limited space, say a habitat, are often mutually correlated, the equivalence is inexact. We will call this principle *the number/density anomaly* (NDA). Of course, immobile eggs and pupae are excepted. General confounding between ostensible mortality and population expansion on the one hand and density increase and population contraction on the other is frequent and insidious. The former occurs typically when the larvae of endopterygotes disperse before pupating (Section **10.2.1**), reducing their density from that on the food resource. Young *Chortoicetes* (Clark, 1947) and *Nezara* nymphs disperse rapidly for food or shelter. Scarabaeine beetles roll their dung balls away from the source (Finn and Gittings, 2003), reducing their progeny's density. Population concentration is also frequent, as when predators concentrate in numbers on their prey: the aggregative response (Section **10.2.3.9**), and when conspecific bark beetles, using an aggregation pheromone, attack an individual tree *en masse* (Section **4.2.1.2(f)**). Seasonal changes in density occur when coccinellid beetles (Yakhontov, 1962; Katsoyannos *et al*., 1997) and *Apion* weevils (Freeman, 1965) concentrate at overwintering sites. Daily changes in density occur in some diurnally active, solitary wasps and bees (Linsley, 1962; Freeman and Johnston, 1978b) and butterflies like *Heliconius charitonius*, when they roost together at night at specific sites (Cook *et al*., 1976). Population density, as a result of movement, can change independently of births and deaths. Note also that a few individuals make up a *small population*, a population with low density is *sparse*. But we must remember that not only do insects use variable amounts of their habitat, but also the suitable and usable areas of their habitat vary with weather, as in *T. paludosa* (above) and *Asphondylia* (Section **12.3.4.3**).

For cereal aphids, Hambäck *et al*. (2007) investigated the link between patch area and density. Following Root (1973), small patches, with their greater ratio of periphery to area, should have relatively greater emigration, whereas larger patches, being bigger targets, should favour immigration. Large patches could also favour immigration by enemies. Is there an optimal patch size? There may be an optimal *density* for r_m, the rate of increase (Section **10.2.2.4**), and emigration may be affected by density (Lidicker, 1962; Enfjall and Leimar, 2005). Hambäck *et al*. (2007), however, found that nutritive *quality* of the patch plays the determining role: the expectation that medium-sized patches should be optimal is fulfilled only when all are providing high quality, a bottom-up effect (Section **10.1**). Generally, *dispersal*, (namely movement between patchy habitats, our *migration*; Section **9.5**), comprises three phases: emigration, transit and immigration (Shaw and Kokko, 2014). But mortality during transit is often a major factor.

While this rationale relates to local populations (Section **12.2.1**), there are also cases on wider spatial scales, as follows. For long-distance immigration to a habitat, those mass migrants that fly high in the air, like aphids and fruit flies, often show sudden increases in density on a crop. If they encounter a cold front they cannot fly further and fall from the sky (Johnson, 1969; Pedgley, 1990). Cold fronts being steep, this occurrence may bring about great population concentrations. It was once thought that *Aphis fabae* (**5.3.1.2(g)**) in England could be controlled by eliminating its spring food plants, the spindle and wayfaring trees, hence breaking the life cycle. But Taylor (1986) and his co-workers at Rothamsted, using numerous suction traps sampling at 40 feet, showed that these aphids could arrive from France in countless billions if weather patterns drove them (Section **10.2.4.5**). Similarly, in many pest aphids, millions of alates fly away from a crop at the end of the season (Johnson, 1969), with emigration massively affecting density.

Then there are statistical outcomes for field studies. Aggregation affects the accuracy of estimating number or density. When animals are spaced regularly the numbers collected in a set of sample units will be similar, giving a low variance and so an accurate estimate. But when estimates are made for patchily distributed animals, such a set gives a high variance and so less accuracy. The relationship of the variance to the mean, over a range of densities, may be used as a *measure of aggregation* (Taylor, personal communication, 1960; Taylor, 1961). This is seen by simply plotting the $\log_{10}$ variance on the $\log_{10}$ mean for several samples. The slope of the regression shows how the species aggregates as density increases (Taylor, 1984). This is known now as *Taylor's power law*, the spatial distribution of a species being a *species-specific characteristic*. Population density, however, is but a crude measure when it comes to assessing the number of contacts both within and between species, namely behavioural interactions (Lloyd, 1967), who proposed the concept of *mean crowding*, a better measure of individual encounter rate.

Spatial hierarchy also affects insect biology (Levin, 1992). *Absolute space* is measured in latitude and longitude, *habitat space* often measured in hectares, and *patch space* often measured in square metres. The entire distribution of a species is its *global distribution* (Sections **9.2, 9.5** and **12.2.1**). Population density can be measured relative to any of these levels (Section **10.2.1;** Blackburn and

Gaston, 1999). Put simply, there is regional abundance and local abundance, and hence regional and local dynamics (Hanski, 1985). But practicalities usually dictate that only patch and/or habitat density can be estimated (but see Freeman and Parnell, 1973; Freeman, 1973a, 1977, 1981a; Hanski, 1998a; Brewer and Gaston, 2003). If habitats are sampled using a stratified scheme (Freeman, 1967b), the sampling stations can be allocated randomly to several patches. When the number of patches is known, the results can be expressed relative to patch or relative to habitat. Low-level space outside the habitat is now usefully referred to as *the matrix* (Ricketts, 2001); it does not include the air above the insect's boundary layer (Taylor, L.R., 1974).

Population can be estimated in terms of *number* and/or *density*. For insects on plants or plant patches, *intensity* may be useful (Southwood, 1978). But density itself can often be measured relative to a plant, e.g. the number of scale insects per metre of branch, even per m^2 of leaf surface (Forkner *et al*., 2004). However, since the density of winter moth larvae (Section **5.2.1.4(g)**), for example, relates to leaf area while that of its pupae to ground area, a common unit is desirable. The aerial density of migrating insects (numbers per unit volume of air sucked through a trap) may be estimated, as in the Rothamsted Insect Survey (Taylor, 1986). *Abundance* can be applied to any of these and so is best thought of as *a generic term that must always be defined*. I use *abundant* to mean *collected in large numbers*. The relative nature of insect density and the NDA are essential points in understanding their dynamics (Section **12.3.4**).

Recently, the factors limiting the geographical range of a species have come into focus (Bird and Hodkinson, 2005; Kokko and López-Sepulcre, 2006; Gevrey and Worner, 2006; Gaston, 2009a and b), studies that have arisen from the potential effects of global warming. But numerous earlier, often unquoted, studies exist (Cook, 1924, 1925; McDonogh, 1939; MacArthur, 1972; Freeman and Jayasingh, 1975a; Freeman, 1976, 1977, 1981a, 1982; Brown, 1984; Rogers and Williams, 1994). Reading only recent papers, students may gain the false impression that spatial aspects of population studies started in the new millennium, culminating in Weintraub and Beanland's (2006, p. 99) naïve assertion: 'Spatial ecology is a science in its infancy'. We see that the core of the subject is implicit in Andrewartha and Birch's three questions that follow Spencer (Section **9.2**). Such studies should be related to the central/marginal model of animal distribution (Wright, 1982a; Brussard, 1984; Yamashita and Pollis, 1995; Section **12.1**). To study most insect and pest insect populations adequately, as Cook and Thompson did in the 1920s, a global perspective of climate, topography, landscape and often plant distribution is fundamental. *Landscape*, a frequent current term, means *an association of adjacent, but often rather different, habitats*. Indeed, plant distribution affects not only herbivores; it diversely affects their enemies and is basic in the ecology of detritivores (see Section **8.2.4**).

9.4 The Species-Abundance Distribution (SAD)

The relative numbers of species sampled at *a location* have a consistent feature, often referred to by this rather woolly term. MacArthur (1960) separated *opportunistic* (often numerous) from *equilibrium* (often sparse) species, a concept later linked to *r*- and *K*-selection (Wallner, 1987; Section **9.8**). But at *a location*, say a given biotope, few animal species are numerous and many more are scarce (Willis, 1922; Huxley, 1942; Fisher *et al*., 1943; Luff, 1978; Hughes, 1986; Hanski, 1998b; Williamson and Gaston, 2005; Matthews and Whittaker, 2015). While this is often addressed in community analysis (synecology), it can also bring a forceful comparative aspect (Section **2.1**) to insect dynamics (autecology) (Taffe, 1979; Jayasingh and Freeman, 1980; Freeman, 1982; den Boer, 1985, 1998; Price, P.W., 1997; Price *et al*., 2011). However, we must distinguish commonness and rarity in a *biotope* from that *regionally* (Hanski, 1982). Comparative work on the dynamics of abundant and rare species, especially congeneric ones, from any spatial scale is infrequent. Even within genera some species are regionally numerous and others sparse (Section **12.3.4.4(e)**) and genetic comparisons between them are rarely made (see Vinogradov, 2003, 2004).

To start locally, if we used a standard method to collect a given insect group in a habitat for a few years, say noctuid moths in a woodland using a light trap, there would be only a few species with many individuals in the sample. We could properly call them 'abundant'. Then there would be many more we could call 'common', meaning found often in moderate numbers. Finally, a large remainder would be rare, meaning collected in ones and twos. If we plotted a series of random numbers, say from 1–50, we would not get this picture: something is going on. For moths trapped at Rothamsted (Williams, 1964), 35 species each had >100 individuals and comprised the bulk of the collection, 205 had 11–100 individuals, while 115 species had 10 or less. But the length of this distributional tail *depends on sampling effort*: all abundant but not all rare species are caught, so affecting the shape of the SAD (Preston, 1962; Freeman and Adams, 1972; Williamson and Gaston, 2005). Data over 3 years on carabid beetles from pit fall traps in a field in north-east England, ranked according to numerical value, show a clear picture (Luff, 1978; Fig. 9.4a).

The ranks here are empirical, relative to each other, to the collection method and to the area sampled. But they can also be displayed as proportions of the total catch (Fig. 9.4b). Both produce decremental curves. From such data indices of diversity, often Shannon's H or Simpson's index (Pianka, 1966; Pielou, 1975; Colinvaux, 1986), may be calculated. MacArthur (1965) suggested that when the habitats sampled are heterogeneous the indices would be persistent and less variable than those for simple habitats (Section **13.1.1**). There is also the feature of *equitability* (Lloyd and Ghelardi, 1964), the *evenness* with which the numbers of each species are distributed (Pielou, 1966). For single-habitat data, some of the tail may result from migrant insects that are, so to speak, 'just passing through' (Lloyd, 1967). Therefore, for many moths such tails are of small interest, as they may well represent non-breeding species. But for habitat-tenacious crane flies sampled comprehensively (Coulson, 1959; Freeman, 1968; Freeman and Adams, 1972), they represent true rarity in the place and period of sampling. While numbers of each species fluctuate between years, the overall pattern across species remains. Here the terms 'common' and 'rare' do not cover *variation in time*; they

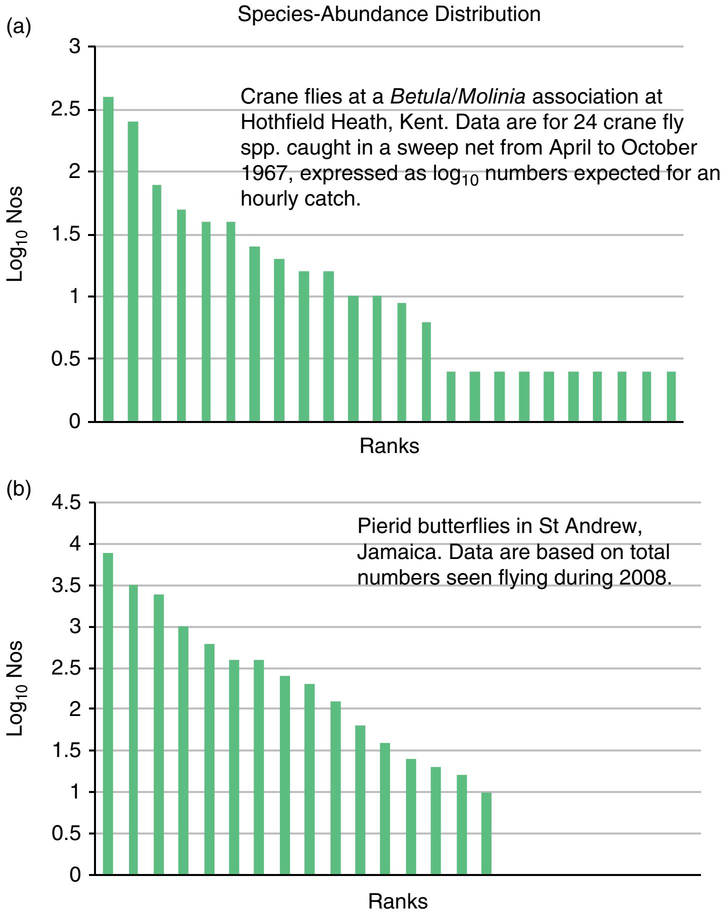


Fig. 9.4. Typical numerical species-abundance distributions. (a) The original data are for the expected hourly catches with a sweep net from April–October 1967 of 24 crane fly species in a *Betula*/*Molinia* association at Hothfield Heath, near Ashford, Kent. (b) The total sightings in 2008 of pierid butterflies in St Andrew, Jamaica.

are averages and so potentially *time independent*. Most SADs are based on numbers collected, but one could also plot biomass distribution (Anderson *et al*., 2012, in Matthews and Whittaker, 2015).

The examples above are from temperate habitats, but insect species contained in complex tropical habitats often show the shape in Fig. 9.5a, which represents a collection I made in 1967–1968 of 171 reduviid bugs in 25 morpho-species from a few hectares of forest in Mato Grosso, Brazil. By contrast, collections from simple biotopes often show the pattern in Fig. 9.5b, with few species and a wide range of densities. The former are characteristic of tropical forests, while the latter are found in harsh montane and sub-arctic environments, and also in some crops. But in the hills of Assam some tea plantations >40 years old contained >200 species, including 41 different coccoid bugs (Banerjee, 1983). Indeed, the montane tropics are normally regionally rich in species, because habitat diversity is multiplied (Section **2.2.2.2**; Pianka, 1966). These are good examples of how comparative ecology can illuminate autecology.

Curve fitting to such data is a common pastime, with the log normal distribution a popular descriptor. Taylor (1978) states that the distribution of the $\log_{10}$ of the N individuals in S species should logically be log normal, and many authors have followed this (Sugihara, 1980; Hughes, 1986; Magurran, 2004). But Williamson and Gaston (2005) give good reasons why this distribution is invalid. Their most serious objection is that 'the log normal distribution SAD implies a log normal individuals abundance curve that in turn implies that there are many abundant species that are not observed'. Some authors (May, 1975; Hughes, 1986) have inferred

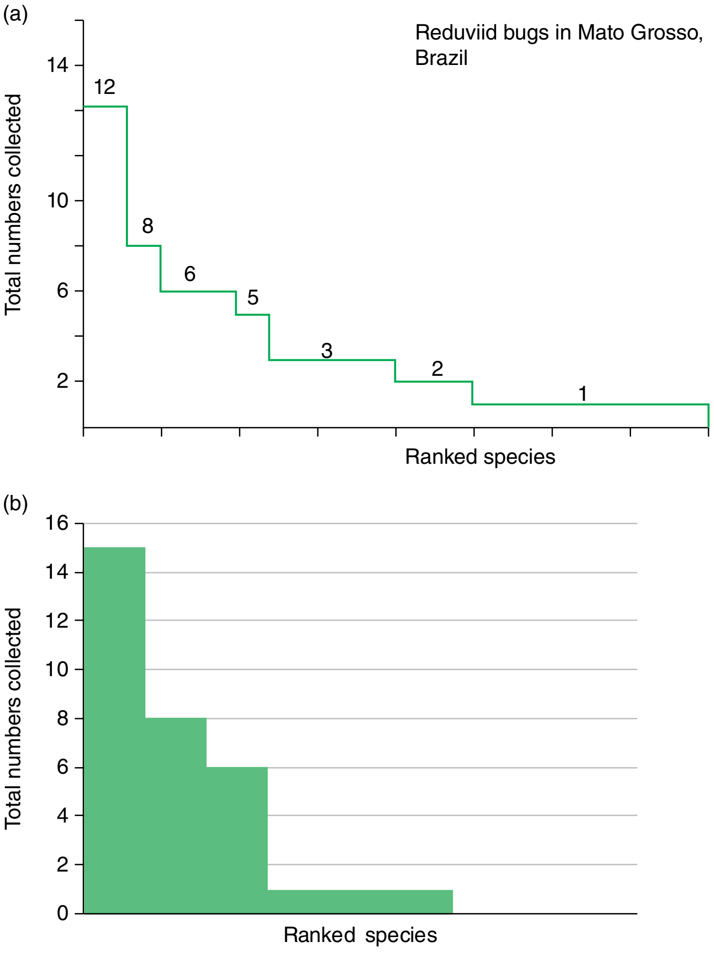


Fig. 9.5. Species abundance in (a) complex plant community and (b) simple plant community. The data in (a) are for 56 reduviid bugs in 16 morpho-species netted on foliage near the Rio da Paz, a tributary of the Xingu, in Mato Grosso, Brazil. The data in (b) are hypothetical.

more (niche theory, interspecific competition) from the exact shape of these curves than I believe is warranted and the effects of migration are often omitted. Certainly for autecology, our interest should centre less on curve fitting, more on what an empirical SAD tells us about insect dynamics, simply because *few species are collected commonly*, *many are rare*.

Even within single biotopes such distributions derive from rather different base data, counts being either *complete* or *incomplete* (Williamson and Gaston, 2005). The former is scarcely possible for an insect fauna but has been done for a forest by counting all the trees. Samples at a site for several years contain more data, while annual, numerical variation of each species is averaged out. Then, data may be approximate as some species are more catchable than others, and because differential longevity also has an effect (Freeman and Adams, 1972; Cowley *et al*., 2001). Larger samples include much of the 'missing tail' referred to above, since more rare species will be found (Krebs, 1972).

But when we come to consider the SAD regionally, rather than locally, many complications arise, as we might suspect. Recall Andrewartha and Birch's question (3) in Section **9.2**: 'Why is it common in this place and rare in that place?'. Our sample for a given species might well cover both places. Even so, a regional collection for several years gives us a better idea of the relationship between numerous and scarce species in an extensive fauna. We compare mean population levels. Such an assessment occurs in faunal keys that give the frequency with which species have been collected. We do not get hard empirical data but we do get information based on long-term, *widespread collecting*, amounting to a huge effort by specialists. The Royal Entomological Society's *Handbooks for the Identification of British Insects* or the *Faune de France* series are examples of such keys. Thus, in the Diptera, Syrphidae, in the '*Handbooks*', a group I know a little as I collected them as a teenager, only 23% of the species are 'common', the rest being 'frequent', 'uncommon' or 'rare'. Some of the 'common' species are not so numerous that >100 of them could be found in a morning: in fact there are only 15 such species (6%). Therefore for *Volucella pellucens*, described as 'common and generally distributed', I know that if I were to search for this beast in southern England on a summer's day I have about a 50:50 chance of finding one. So, we could say that ~94% of British syrphid species are sparse. Rarity, rather than abundance, is the rule (Darwin, 1859). SADs have been related to the core and satellite species concept (Hanski, 1982; Gotelli, 1991; Matthews and Whittaker, 2015). The chrysomelid fauna of Hungary is well known, but 48.5% of them come from only a few specimens or localized habitats (Kaszab, 1962, in Jermy, 1984). Furthermore, most herbivores have low densities in relation to their food plants (Crawley, 1989). For parasitoids, Miller (1966) records 38 species attacking *Acleris variana* (Section **5.2.1.4(g)**) in eastern Canada, of which 12 are common and 26 are rare. But of course these parasitoids may each have many other hosts; the sample is incomplete.

So, the basic question for insect dynamics arising from the SAD is: 'Why are so few species abundant?' or better still, 'why are commonness and rarity so distributed?'. This has been appreciated for a long time. In 1859 Darwin (Chap. 11) wrote, '... for rarity is the attribute of a vast number of species of all classes, in all countries'. Preston (1962, 1980), Pimentel (1968) and Gaston (1994), among others, have considered the subject in detail. A simple view is that species having large, dense populations are limited by resources, those with small, sparse ones by enemies (Hanski, 1985). We therefore feed huge populations of herbivorous pests with our crops. Conversely we ask, 'Why are there so few pest species?'. Many farmers would disagree vehemently, but of perhaps several million insect species that exist (Section **1.3**), most of which are yet to be described or will go extinct before they are, there are under 2000 important pest species worldwide, <0.1% of the total. Further bias arises since pests are well known, unlike most of the remainder (Evans, 1970). Pedigo's (1996) exhaustive list of North American pests comprises ~1700 species, but he states that only ~600 of them are significant. Of course, many potential pests are restrained by enemies (Stern *et al*., 1959; Colinvaux, 1986; Berryman, 1999). Major crop pests are usually fewer than minor ones. For wheat the numbers are 10:61, for apples 13:65 and cotton 28:62, but for rice the ratio is 49:48 (van Emden and Service, 2004). This is odd, although rice paddies (Section **13.3.2.2**) more resemble natural ecosystems than most other crop environments. Approximately 300 pests are known for stored products, but only 18 are 'of primary economic importance' (Boyer *et al*., 2012).

The regional SAD, then, is of economic interest because only abundant species may be serious pests. Here *commonness* relates to the quantity of the food resource consumed, as Andrewartha and Birch defined. While rare species occasionally become abundant as the years pass, especially in crop situations with new high-yielding but susceptible cultivars (bottom-up), or because of the misuse of insecticides which kill the pests' enemies (top-down), or in continents into which they were introduced (Elton, 1958; Williamson, 1996; Niemela and Mattson, 1996), the SAD is a firm relationship. Rare species usually continue to be rare and abundant ones continue in their abundance for many generations (Lawton, 1999). These terms are *time independent*. But some 'abundant' species (spruce budmoths, mountain pine beetles), form *outbreak* (*eruptive*) *populations* (Pimentel, 1961; Wallner, 1987; Hunter, 1991; Berryman, 1996; Price *et al*., 1998; Safranyik *et al*., 2010) that remain sparse between outbreaks.

Another comparative feature of commonness and rarity is interesting but rarely discussed. Some insect groups have a greater proportion of common species than do others, although we could relate this to *r*- and *K*-selection (Colinvaux, 1986; Wallner, 1987). Pierid butterflies therefore contain many common species while hairstreaks (Theclinae) have few. In the UK there are ten pierid species, five being common. In Jamaica there are 20, and 11 are common. While pierid butterflies worldwide are less numerous in species than Lycaenidae, they are more numerous in individuals (Ehrlich and Raven, 1964). None of the five British hairsteaks or the 12 Jamaican ones is common in any sense. More strikingly, in the Indo-Australasian tropics there are ~200 species of the thecline genus *Arhopala*, but almost all of them are rare (Vane-Wright, personal communication, 2009). Similarly, the ~30 species of giant skippers (*Megathymus*) of the southern USA are all scarce (Emmel, 1991). Then in the Diptera Tipulidae, Culicidae and Simuliidae, many species are abundant at times, while in the British Conopidae and Stratiomyidae, they are in my experience infrequent. Many acridid species (Section **5.2.1.1**) form outbreak populations but the related Tettigoniidae do not (Price, 1997). Tenthredinid sawflies have a higher proportion of eruptive species on conifers than on angiosperms (Price *et al*., 2005). These are just a few examples: *r*- and *K*-selection is not the full story.

Some of these features relate to the group's trophic position: large predatory insects are scarce (Wiens, 1989; Griffiths, 1992; Blackburn and Gaston, 1999). Mean estimated density of females of the big solitary wasp *Zeta abdominale* was ~6/ha (Taffe, 1983) in contrast to that of outbreaking forest moths at >1,000,000/ha (Section **11.3.1**). Thousands of thrips can subsist on a tomato plant, which could briefly feed a single *Manduca* larva (Section **5.2.1.4(i)**). Scarcity also relates to specificity for resources (Thompson, 1956; Brown, 1984; Hanski, 1998b). Most pierid and hairstreak larvae are rather small, exophytic herbivores. In Britain, at least, their food plants are ubiquitous. In contrast to many itinerant, conspicuous *Pieris*, however, several hairstreaks are secluded, forest canopy species, which affects catchability and may bias our judgement. Generally, we should seek answers for the form of the SAD in a regional study of insect dynamics (Section **12.3**), doubtlessly in their genetics and probably in their mode of speciation (Section **12.3.4.4(e)**).

There are cases where small, ancient groups are poor in species and have cryptic lifestyles. For cave-dwelling invertebrates in general, Vandel (1965) suggested that many archaic species, having entered a phase of 'sénilité phylétique', retreat to these depths as a refuge from the intensity of competition from surface forms. While his argument marshals no Darwinian basis, it is obvious that, for example, most Apterygota have such lifestyles – but they may be abundant. The Exopterygota also have a few small orders, such as the Embioptera, with cryptic habits, while even termites, although highly successful in the tropics, remain hidden (see Section **12.4**). Hamilton (1978) discusses arthropod evolution in such situations. Of course, locusts and dragonflies provide glaring exceptions.

Then there are macro-ecological aspects. For British butterflies, wide distributions are associated with high mean density (Cowley *et al*., 2001; Section **12.3.4**). Another aspect is that most insects isolated on the far edge of their distribution are rare, specialized and ultimately often fail to sustain a breeding population. The butterfly *Papilio machaon* is common and widespread in Eurasia, more local in France, but rare and restricted in Britain (Ford, 1946; Dempster *et al*., 1976), where it eats but a single food plant. It became extinct at Wicken Fen, Cambridgeshire, UK, in the 1950s although a population persists in marshy parts of the Norfolk Broads. In Fennoscandia, it eats 21 plant species. It penetrates Eurasian deserts and feeds on a succession of food plants (Buxton, 1923). Then there may be *connected* sink populations where deaths exceed births. In the wasp *Trypoxylon palliditarse*, in the wet montane valleys of northern

Trinidad, these are maintained by immigration from the lowlands where births far exceed deaths (Freeman. 1981a; Section **12.3.4.3**).

Related to the SAD, is the *number of habitats* in which species are found. This graphic is typically U-shaped (**Fig. 9.6**; Brown, 1984; Hanski and Gyllenberg, 1993). Species usually occur either in few or in many habitats or patches. Bumble bees in Poland (Fig. 1 in Hanski, 1982) illustrate this. Such distributions result from there being generalist and specialist species; the former being found in many habitats, and vice versa (Brown, 1984), an idea following Thompson's theory (Section **11.2.2.1**) and Hanski's *core and satellite species* concept. Core species have large numbers (*N* is big) in a high proportion (*p*) of habitats (or patches). *Pieris brassicae* in UK and *Ascia monuste* (Pieridae) in Jamaica are examples. Hanski pointed out that satellite species show *three types of rarity*: type 1 *N* is big but *p* small; type 2 *N* is small but *p* big; and type 3 both *N* and *p* are small. Both *N* and *p* vary with time. But when wide temporal variation in numbers exists in a very local species, as in *Eurytides marcellinus* (Section **12.3.3.2**), rarity changes between type 1 and type 3. While herbivorous insects on bracken give little support for the core-satellite hypothesis (Gaston and Lawton, 1991), in general these aspects of rarity in satellite species remain a useful concept.

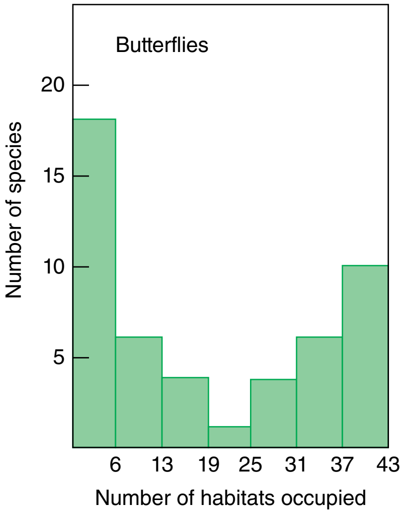


Fig. 9.6. U-shaped distribution of number of habitats occupied by different species. Adapted from Hanski, I. (1991) Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society* 42, 17–38. Reproduced with permission.

Related to Andrewartha and Birch's first question (Section **9.2**), the frequency distribution of *range sizes* of different species is a recent inquiry (Brown *et al*., 1996; Gaston, 1998, 2009b; Gavrilets *et al*., 2000; Section **12.3.4.1**). Rather as in the SAD, few species have large ranges and many have restricted ones. But in the long term, evolutionary complexities exist: range sizes depend primarily on speciation and extinction (Section **9.10**), and for insects especially, migration and the ability to colonize, adapt and survive in new environments are additional factors. Then, species with small to medium ranges are more likely to speciate, while risk of extinction declines with increasing range size.

Why are there, comparatively, so few pest species? By any definition rare species are never serious pests, but most abundant species are not pests either, simply because they do not attack people, livestock or crops. As we have seen, few species of any sort are numerous. Out of ~60 British butterflies only one, *Pieris brassicae,* is a regular pest, although *P. rapae* can be a minor nuisance. Of the Jamaican mosquito fauna comprising ~60 species, only three are known to be disease vectors although a lot more bite humans. In aphids, a family containing several notorious pests, there are ~4400 species globally but <100 (2.3%) are pests, many being of little economic significance (Eastop, personal communication, 2002). In North American Cerambycidae (~1200 species), only 36 (3%) are given as pests in Pedigo's (1996) exhaustive list, while only 3 of the 90 known Japanese plant-hoppers are major pests of rice (Kisimoto, 1984). Only 7 of >200 known *Anastrepha* fruit flies are significant pests (Sivinski and Aluja, 2003). One obvious reason for this situation has already been noted (Section **2.1**): while insect herbivores are mainly oligophagous (Bernays and Graham, 1988), major crop plants are found in *only 10 out of the 250 higher plant families*. But, as usual, other reasons are contributory. Hoffmann *et al.* (2008) note that a high proportion of pest species are parthenogenetic.

In relation to natural control, Price *et al.* (1998) remark: '... a comparative macro-evolutionary approach to insect population dynamics could encompass all species on a gradient from rare and/or latent, to common and/or eruptive'. But few studies exist on the dynamics of rare species (Taffe, 1979; Hanski, 1990), although work by Eickwort

(1977) on the beetle *Labidomera clivicollis*, by Ittyeipe and Taffe (1982) on the wasp *Monobia mochii*, and on two rare swallowtails, *Papilio homerus* (Garraway *et al*., 1993a, 2008) and *Parides burchellanus* (Beirão *et al*., 2012), are exceptions. Wallner (1987) and Hunter (1991) have compared the ecologies of outbreaking and non-outbreaking species. Of course, outbreaks occur when births greatly exceed deaths but the reasons for this are multiple. They include sustained suitability of the physical environment and the ineffectiveness of enemies. In population genetics too, few, mainly abundant species, have been investigated (Blows and Hoffmann, 2005). This whole area poses considerable intellectual stress, partly because making accurate estimates of births, deaths and redistribution in rare species is difficult, but also because of the challenge of relating novel empirical data to established evolutionary and genetical theories, which are generally couched in simplified models.

Some probable causes for rarity are exclusively genetic (Vinogradov, 2003, 2004). Over evolutionary time genetic rubbish builds up in the genome (Trivers, personal communication, 2008), especially that due to *selfish transposable elements*. These are 'essentially parasites on an organism's genome' (Endler and McLellan, 1988). Vinogradov found such ostensibly useless material to be greater in endangered plant and vertebrate species. Were this true for insects, it could contribute to the distribution of rarity found in SADs, that is, rare species having larger genomes with a greater proportion of selfish elements. They would find fewer favourable sites for their limited adaptive abilities (type 3 rarity). Indeed, coccinellid beetles with large genomes have slow developmental rates (Sloggett and Honěk, 2012). Rarity could result from both speciation and degradation. We link these conjectures to the genetic modification of pests to suppress them (Burt, 2003; Section **13.2.2.2**). Then, in small isolates genes and genetic variability may be lost, albeit slowly, by RGD. A plausible stepping-stone model (Gavrilets *et al*., 2000) gives further insight to SAD: species with small populations and poor powers of redistribution should have higher speciation rates. If this process were not overwhelmed by higher extinction rates, it would increase the frequency of rare species and produce the long tail in SAD (see Sections **12.3.4** and **12.4**).

Finally, the density of a species has *primary and secondary effects* on its dynamics. The primary effect, apart from cannibalism, is *intraspecific competition* for a limited resource (Section **10.1**). Secondary effects are twofold. First, there may be *interspecific competition* with another species for a scarce resource (Section **9.8**). Both types of competition are behavioural endeavours that may result in mortality that is often density dependent. Second, the high density of the focal species itself may attract enemies resulting in mortality (Section **10.2.3.9**) that may or may not be density dependent.

9.5 The Patch, Habitat, Population and Redistribution

Environmental space is treated extensively in Section **12.2**, but here we introduce it as it is basic to autecology and leads to a firm base for examining *redistribution* (q.v.; Section **10.2.4**). Historically, an inadequate definition of 'habitat' has been one of the blind spots of zoology (Elton, 1966), while Berryman (2002), following Richards (1961), regards 'population' as central to ecology. The 'lack of precision' in defining population in models makes them hard to interpret in the field (Harrington and Taylor, 1990). Johnson (1969) remarks that '… the terms habitat, territory and population reflect imprecise concepts that hinder the study of population dynamics'. But the habitat concept in nature, vaguely and variably defined, has had a hallowed use from the time of Spencer (1864). Generations of ecologists have recognized its utility. The SOED defines habitat as 'The natural environment characteristically occupied by a particular organism' (Anon, 1993), an *autecological definition*. The concept is essentially English: the obvious patchwork of woodland 'habitats' left between fields there, often resulted from the 'enclosures' of previous centuries (Hoskins, 1955). For *synecology*, Elton and Miller (1954) present a complex view of habitats, recognizing 'formation types' (e.g. field, scrub, woodland), edge effects and vertical layering. Andrewartha and Birch (1954) do not use 'habitat' (Latin = *it inhabits*) in autecology, but '*a place in which to live*'. This is long-winded and vague spatially. Unsurprisingly, ecologists have not taken it up. Habitat is properly *'relative to the focal species'* (Wiens, 1976; Cornell and Lawton, 1992). For many pests habitats are co-extensive with the crop attacked, for example a wheat field infested by wheat bulb flies or apples riddled by codling moth larvae in an orchard. These are environments modified by man that, due to husbandry, show uniformity and possess clear-cut boundaries.

Definition is simple, although with crop rotation such habitats change materially or disappear.

Natural habitats are also generally co-extensive with definable biotopes. They also change *in time* (Section **12.2.6**), albeit slowly, especially if not in the climax sere (Section **2.2.3**) and/or are prone to human interference. We refer to the same ecological entity *relative* to our study: oak woodland is a *community* or *biotope* (synecology) that is a *habitat* for winter moths (autecology). Habitats show both horizontal and vertical spatial heterogeneity (Elton and Miller, 1954; Ovington, 1962; Wiens, 1976; Terborgh, 1985). They have dimensionality; forest has a greater vertical component than, say, moorland (Zera and Denno, 1997). Vertical stratification is driven by light penetration (Terborgh, 1985), while horizontal changes along transects often stem from natural discontinuities or gradients in geology and topography and on a wider spatial scale, in climate. Biotopes are influenced by *edaphic*, *topographical and climatic factors,* and including these function as *ecosystems* (Tansley, 1935) with characteristic properties. Thus woodlands have, both diurnally and annually, more stable hygrothermal properties, less light and lower wind speeds than adjacent fields. They have a flora, by which they are readily recognized, but also a characteristic if less visible fauna. Such communities have much spatio-temporal concordance and many, but certainly not all (Cornell and Lawton, 1992), of their members interact (Askew and Shaw, 1986; Wootton and Emmerson, 2005). Their boundaries can be as sharp as those in agriculture, such as that between gallery forest and grassland in Amazonia, this being due to a sudden change in soil fertility. Here at noon, grasslands may be ~10°C warmer and ~30% less humid than the adjacent forest (see Uhl and Kauffman, 1990). But other biotopes intergrade along a transect as in two types of savannah from this region known as 'cerrado' and 'cerradão' (= big cerrado), a change associated with gradually increasing soil moisture. We see that a *biotope* as a *habitat* focuses on herbivores, while their enemies follow in train. But in all, natural habitats are harder to define than those in agriculture, as we will also see.

Biotopes form the fine structure of biomes (Section **2.2.3.1**). In autecology, these communities function as *habitats* or *lebensraum*, loosely regarded as 'living space' (Corbet, 1999), relate to many insect species so forming the stage on which the innate attributes of individuals and environmental factors affecting them interplay. But they normally use only *part* of a biotope. Johnson (1969) says '… a breeding habitat is where the eggs are laid, larvae develop, and adults emerge'. Following this, Southwood *et al.* (1974) define habitat as 'the area accessible to the trivial movements of the food harvesting stages'. It is a 'templet' against which ecological strategies are selected (Southwood, 1977; Section **11.2.2.5**) and contains all resources necessary for growth, reproduction and survival. But a better term (Section **9.3**) for this restricted spatial level is the *patch* (Hassell and Southwood, 1978). This removes several problems in defining *habitat*, whose structure arises from an assembly of smaller scale, unequal units (Levin, 1992). In summary, patches describe *habitat heterogeneity* (Section **12.2**). *Ula sylvatica* (Tipulidae) flies in woodland (the habitat), but breeds only in fungal fruiting bodies (patches) therein. Sympatric species may still be partly isolated because they breed in different patches (i.e. they have different niches), although adults share the same larger space. If a given patch type is used by a species in adjacent plant communities its distribution is in the *landscape*. *Phytomyza ilicis* mines holly leaves not only in woodlands, but also in hedgerows (Heads and Lawton, 1983).

A further complication is that many insects do not breed in specific habitats. Apart from *P. ilicis* and similar miners, they include many aphids and pierid butterflies. A given biotope, even if clearly defined, does not encompass their entire breeding space, they follow *plant* distribution. Then, not all such biotopes are distinct from adjacent ones, as in cerrado and cerradão. With pests of field crops, there may be 'reservoir populations' (Section **13.1.2.2**) elsewhere, usually in related or 'volunteer' plants. A way to resolve this difficulty is to recognize *landscape species*, or if you wish, *multi-habitat species*. This retains the link between 'biotope' and 'habitat'. Of course, multi-habitat species form *metapopulations*. Indeed, metapopulation and landscape concepts can be applied to all levels from patch upwards. Overall, resource distribution determines the *potential distribution* of a species, this being essentially time independent.

By contrast, '*niche*', at its simplest, refers to what an animal '… is doing … its relations to food and enemies' (Elton, 1927) or for synecology the 'functional relationships of a species within a community' (Whittaker *et al.*, 1975). It is a 'job' rather than a 'place', a 'profession' not an 'address' (Andrewartha and Birch, 1984). More comprehensively, for any species it is 'the outward projection of its needs'

(Mayr, 1963, p. 78). Two potentially competing species may occupy the same habitat or even patch, but have different niches. In synecology, a more extended concept of niche is commonly applied. This includes components such as body size, innate attributes, defensive behaviour *and spatial distribution*, an obfuscating mélange in autecology (Sections **9.2** and **10.1**).

Richards (1961) defined population as:

> … all those individuals of one species whose lives are sufficiently integrated to have an influence on one another. A population will normally occupy a fairly well-defined area even though the distribution of a species is hardly ever strictly continuous [i.e. they are metapopulations]. Although populations so defined will often tend to have somewhat woolly edges, it is only to such populations to which one can correctly attribute such features as birth rates and death rates.

Stern *et al.*'s (1959) definition is simply 'A group of individuals of the same species that occupies a given area'. But what is 'a given area'? Turchin (2003), following Berryman (2002), uses a broad definition of population suiting his temporal approach to dynamics, which I paraphrase as:

> a group of conspecific individuals occupying an area big enough [i.e. several km^2] to permit normal redistribution, where population changes are determined largely by births and deaths. Sub-groups living in smaller areas are *local populations*, whose dynamics are strongly affected by redistribution.

But this apparent solution glosses over the fact that mortality during population redistribution is often the *major numerical factor* (Freeman, 1973a, 1976, 1977, 1981a, 1982; Taylor, 1977; Watmough, 1983, Freeman and Geoghagen, 1989; Freeman and Ittyeipe, 1993; Kisimoto and Sogawa, 1995; Ward *et al.*, 1998). Its effects can be teased out from overall juvenile mortality only by special methods (Section **11.4.2**). Then again, larger areas have greater environmental heterogeneity, leading to diverse dynamics and perhaps a wealth of sampling problems in empirical work (Section **9.3**).

My definition is: 'Insect populations occupy habitats or landscapes and their reproduction and development within them occurs in patches'. And, following Richards, 'The lives of the individuals there must be integrated sufficiently to allow valid estimates of birth and death rates. These estimates must not be compromised by redistribution'. This works well for many herbivorous pests and for most insects in 'natural' habitats, perhaps not so well for a few vagrant species such as aphids, Pieris butterflies and many mosquitoes. But insects do not occupy all ostensibly suitable habitats at any time (Spencer, 1864; Thompson, 1929; Andrewartha and Birch, 1954). As above, assemblies of adjacent local populations are 'metapopulations' (Levins, 1970; Wilson, 1975; Cronin and Reeve, 2005) that occupy patchy habitats (Section **12.2.1**). As above, agricultural pests frequently have 'reservoir populations' (Section **13.1.2.2**) that subsist on volunteer plants, plants related to the crop and weeds, so forming metapopulations with a heterogeneous resource base. All the individuals of a given species comprise its global population (Section **9.2**).

Redistribution is complex both in scope (Turchin, 1998) and function, but having defined habitat, it is straightforward to define *movement between habitats as migration and movement within them as dispersal* (Hassell and Southwood, 1978; Weisser and Hassell, 1996). Indeed, the SOED defines 'migrate' as 'to go from one habitat to another'. But the distinction rests on defining habitat. For Kennedy (1961b), migration is persistent, undistracted, straightened-out movement. Dispersal often implies movement away from an area of high density, resulting in its reduction, the 'kind of population redistribution ... that leads to spatial spread' (Turchin, 1998). It involves the separation of individuals (Taylor, 1986). A general case is when mature larvae leave their food resource and so avoid potentially high pupal density (see Section **10.2.1** for *Pieris*). They move in two sequential phases: (i) after *undistracted dispersal* they show (ii) *appetitive movement* to seek pupation sites. The latter is not part of dispersal (Johnson, 1969). When aggregation occurs as an outcome of movement, it is usually a result of seeking resources, mates and/or other conspecific individuals, so resulting from mutual attraction, and often employs an aggregation pheromone. Dispersal affects local, within-habitat density, whereas migration affects regional distribution and beyond (Gatehouse and Zhang, 1995; Gripenberg and Roslin, 2007). Do not confuse *dispersion*, as do Wade and Goodnight (1991) and others, the spatial distribution of objects *at an instant*, with the dynamic process of *dispersal* (Taylor, 1984). Flight spanning hundreds of kilometres, as in brown plant-hoppers, is simply *long-distance migration*. These bugs abandon their 'station-keeping' behaviour and are massively displaced in relatively straight paths on seasonal winds (Drake and Gatehouse, 1995). Migration is revealed not only by the mass arrival of flying insects when no juveniles had been present, but also by the absence of adults when there had been many juveniles. While all insects redistribute, many do not migrate. Examples in the UK include the butterfly *Papilio machaon*, the moth *Callimorpha dominula* (Goulson and Owen, 1997) and many Tipulidae (Freeman, 1968; Section **12.3.4.4(c)**). See Taylor (1986) for a more detailed appraisal.

9.6 The Population and the Individual

A biological population comprises interacting, conspecific individuals in the same locality at the same time. As time passes, its individuals are replaced by their progeny, subject to selection, chance and often to migration. Therefore the genes it carries, its innate properties and often its spatial distribution change in time (Taylor, 1986; see Fig. 9.5; see also Robinson, 2004; Barker and Wilson, 2010). Taylor and Taylor (1977) likened a population through time to the interwoven stele of a fern: the cross section representing space and the vertical dimension time (Fig. 9.7). But a population is a human construct, there is no population without individuals. It exists as a collectivity but is unified only in the mind, and only there exists as an entity (Thompson, 1956). In about 1750, the Comte de Buffon pointed out that individuals alone exist in nature, while genera, orders, classes exist only in our imagination. These views have even earlier origins: as to the nature of the Holy Trinity by Roscelin, the first scholastic philosopher, in a letter to Abélard in the eleventh century: a Population of Three! (Copleston, 1957, p.142). They have been held a long time. So, when Haeckel (1866) defined ecology as 'Ökologie ist die Wissenschaft von den Beziehungen des Organismus zur umgebenden Aussenwelt' (ecology is the science of the relationships of the organism to the surrounding world), he used the singular, not the plural (der Organismen). The logic of individuality initially escaped Wright (1931, p. 98) who stated: '… the evolutionary process is concerned, not with individuals, but with species …', this despite the above and that Fisher (1930) had shown that many examples of adaptation were explicable only by selection on individuals. That being said, we see that Haeckel's definition is closer to *autecology* than to *synecology*.

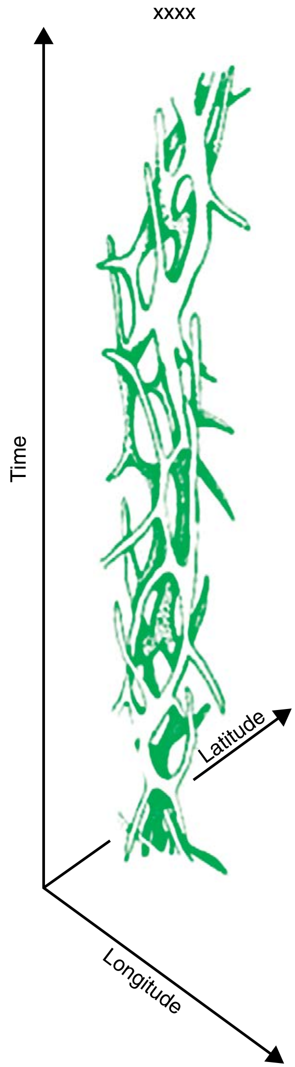


Fig. 9.7. Taylor's stele. The figure models the shifting nature of the distribution of vagile insects, the vertical component representing time and the lateral one space. But not all insects have such populations. Adapted from: Taylor, L.R. and Taylor, R.A.J. (1977) Aggregation, migration and population mechanics. *Nature* 265, 415–421. Fig. 1, p. 416. Reproduced with permission.

Making individuals the primary focus (Thompson, 1956; Williams, 1966; Trivers, 1985; Bolnick *et al.*, 2003) allows their interactions within a population to be considered (Andrewartha and Birch, 1954, p. 14). The concept is employed in population mathematics and termed '*methodological individualism*' (Turchin, 2003), and was promoted by Descartes' (1596–1650) philosophy of the individual. The idea is extended to the community and the ecosystem (Parker, 2004; Hawes *et al*., 2005), although not for the first time (Gleason, 1926; Dice, 1952). Thus, *for a given individual all other individuals in the population (or the community and ecosystem) are potentially part of its biotic environment*. A population can be regarded as an *entity* providing it is not viewed as independent from the individuals comprising it and their inter-relationships (Goudge, 1961). So, relationships between individual and environment are *primary*, those between population and environment are *secondary*. Some ambiguities encountered in discussing competition (Section **9.8**) arise from disregarding this distinction. While competition concerns primarily the behaviour of two individuals, it may or may not engender significant consequences to the population. Some processes and patterns resulting from individual acts, however, are discernible only in such groups (Levin, 1992).

Individuals forming a population at any time vary in stage, age, size, sex, behaviour, polymorphic traits (Section **1.4.3**), rate of development, ability to survive a given physical stress, and so on (den Boer, 1998; Roff, 2002; Schuett *et al*., 2015). Much variation is adaptive (Hamilton, 1996; Wilson, 1998). Instars relate to age, as they follow in a fixed sequence (Section **1.3**). A population is what it is because of *the variable nature of individuals comprising it*. They are not 'created equal'. For simplicity, many models assume them to be identical (Łomniki, 1980, 1988; Bolnick *et al*., 2003; Benton *et al*., 2006; Section **11.5.1**). But models are 'sensitive to the assumption of individual equality' (Bjornstad and Hansen, 1994) and to population sub-division (Sugg *et al*., 1996). It follows that adult size affects key traits like AF (Richards and Waloff, 1954; Freeman and Johnston, 1978a; Honĕk, 1993; Ohgushi, 1996; Fox and Czesak, 2000; Section **10.2.5.2**), their survival (Freeman, 1981c; Ohgushi, 1996; T. Price, 1997; Section **9.1**) and even that of their offspring (Seidelmann, 2014). For males, size (Juliano, 1985; McLain and Shure, 1987) and shape (De Block and Stoks, 2007) often affect mating success.

But there are more subtle effects. When a sample of a species is exposed to a given degree of extreme cold, not all individuals will die: they do not all have the same resistance (*cold hardiness*) to such stress. On a wider scale, populations from different regions within the species' distribution may also vary in cold hardiness, as in the overwintering eggs of *Locusta* in north and south China (Jing and Kang, 2003). They also vary due to different low temperatures that individuals have experienced previously, referred to as acclimatization (Mellanby, 1939; Section **10.2.3.3**). This can occur even within a microhabitat (Freeman, 1967b; Danks, 2007). In short, genetic and phenotypic plasticity are at work (Birch, 1960), along with the influence of inherited environmental effects (Rossiter, 1996; Bonduriansky and Day, 2009; Section **11.2.3**). Therefore individual optima for growth, survival and fecundity vary. While *individuals* attempt to track their physical optima, such factors change in space and time (Thompson, 1956; Fox and Czesak, 2000; Section **11.2.2.1**).

Most theorists agree that the individual is the focus of evolution by natural selection (Fisher, 1930; Birch, 1960; Lewontin, 1970; Berry, 1985; Trivers, 1985; Wilson, 1983, 1997; but see Feldhaar, 2011, and Section **10.2.2.6**). Dawkins (1989) addresses selection at the genic level, genes being potentially immortal. It rarely acts on the population directly (*group selection*), nor on the species, except in rather unusual circumstances. Back in 1929 Thompson remarks '… organisms multiply without any regard to the interests of the species as a whole'. But Wilson (1983, 1997) and Gilbert (1984) warn us wisely to keep our minds open. Facile simplification is always a danger (Chamberlin, 1897). Polis (1981) refers to group selection as a genetic explanation of some forms of cannibalism. In the context of the fossil record Maynard Smith (1983a, 1983b) uses the term 'species selection'. Rogers (1990) and Hanski (1998b) implicated group selection within some metapopulations. In non-migratory species, local adaptation can produce successful strains, with less successful local strains dying out. Group selection is also possible in some forms of symbiosis. But functional organization at any level requires natural selection *at that level* (Williams, 1966; Wilson, 1983; Sapp, 1994). Group selection, should it occur, should be called *inter-group selection*. There must always be heritable phenotypic variation in *group fitness*. But since selection between individuals is so strong (Berry, 1985), what happens in populations is *usually* the aggregate result of what happens to the individuals comprising it (den Boer, 1968; Slatkin, 1987). They act not 'for the good of their species', but for their own good (Williams, 1966, 1971; Ghiselin, 1974). The 'good' referred to is RS, largely the ability to maximize their gene flow to posterity. But genes integrated in individuals do not always act for the corporate good, a transgression referred to as *genetic conflict* (Burt and Trivers, 2006, q.v.).

We now consider 'fitness', which relates to different genotypes expressed in the individual phenotypes for which they code. The *relative* numbers of offspring in the following generation *or generations* determine fitness (Hamilton, 1967; Crow and Kimura, 1970; Wall and Begon, 1985). Hardy (1992) regards a mother's fitness as maximized by her producing the *largest number* of fertilized daughters. But there may be an option of producing a few fit (large) daughters or more less fit (small) ones (Smith and Fretwell, 1974; Freeman, 1981b; Jervis and Kidd, 1986; q.v.). As Fisher (1930, Chap. 6) remarks: 'The success of an organism … is not measured only by the number of its surviving offspring, but also by the quality … of these offspring'. Namely, quality in quantity. The *inclusive fitness* of a reproductive is compounded of fitness due to its own reproduction plus that of its relatives devalued by their genetic distances (Hamilton, 1964), genes being *identical by descent* (q.v.). That of sterile castes is due only to reproduction in relatives. Fitness is also *relative* to how the rest of the population performs at the same time. But the final imperative for a selfish gene (Dawkins, 1989) is *to avoid going extinct* (MacArthur, 1972; Thompson, 1983). So there is some selection at the genic level (Maynard Smith, 1983b; Dawkins, 1989). See Maynard Smith (1964, 1976, 1983b), Williams (1966), Murray (1988) and Costa (2013) for lucid discussions of selection and fitness, and Section **11.2.2.1**.

Fisher (1930) noted that fitness, or 'adaptedness', tends to equilibrium between the positive force of natural selection and potentially disruptive forces of mutation and environmental change. The degree to which populations can respond in a given direction is proportional to their *additive genetic variance* (Bürger, 1999; Conner, 2003; q.v.). Fitness distributions shift continually (Burt, 1995) but relate only to what *happened in the past* (Kirkpatrick and Lande, 1989). Species cannot anticipate the future so selection always plays 'catch-up' (Fisher, 1930; Price, 1972; Gilbert *et al*., 2010). They are 'prisoners in their own evolutionary history' (Southwood, 1988).

Therefore 'variation in the quality of individuals in a population is too great to ignore safely, and should wherever possible be incorporated into studies of their population dynamics' (Łomniki, 1988; see also Leather and Awmack, 1998; Roff, 2002; Schuett *et al*., 2015). Also, 'heredity is not exact' (Maynard Smith, 1983b); without this inexactness evolution would ultimately cease. 'Nature, … greatly values variation of all kinds within her units, does so at all levels, and seemingly goes to great lengths to protect it' (Hamilton, 1996; see also Wagner, 1996). Individual variability can be expressed: (i) within a sibling group; (ii) within a population; and (iii) between populations, often relating to regional effects, and may just possibly involve inter-group selection. Recall too that gene expression can be affected by physiology, as in the classic case of baldness and testosterone levels in men. Similarly, the *for* gene, which controls foraging activity in honey bees, responds to conditions within the hive (Ben-Shahar *et al*., 2002). But not all that is inherited is Mendelian (Kirkpatrick and Lande, 1989; Rossiter, 1991, 1996; Section **11.2.3**). Parental influences, especially maternal ones, also have complex effects, ones stemming from the preceding generation. And while we focus mainly on individuals as the units of selection, they cannot be regarded free of their symbionts (Feldhaar, 2011; Moran, 2015).

Individual quality varies greatly. Therefore if all larval individuals in a *Tipula* spp. population were identical genetically and had the same environmental history, a test of cold hardiness, say −5°C for 10 hours, might kill none of them but one at −6°C for 10 hours might kill all of them (Section **10.2.3.3**), with no spread of resistance existing. But in nature such differences might result in a mortality distribution from 5% at −2°C to 95% at −8°C. Again, individual differences result in population outcomes. But more subtle ecological results arise from genetic variation. If unfit hybrids are being formed as a result of immigration into a population well adjusted to its habitat, these might well have lower RS after suffering inimical factors. Hybrid inferiority comes into play in parapatric speciation (Dobzhansky, 1940; Schluter, 2001), and would have even greater interest should sympatric speciation (Maynard Smith, 1966) prove to be more general than is often thought (Bush, 1994; Via, 2001; Bolnick and Fitzpatrick, 2007; Peccoud and Simon, 2010; Section **9.10**).

Finally, we consider some evolutionary implications of sexual reproduction. Compared to asexual reproduction, the sexual mode has a twofold cost in genetic fitness (Williams, 1975; Maynard Smith, 1978). If a gene suppressing meiosis was passed to offspring with certainty, not a 50% chance as in sexual reproduction, it would enjoy the same fitness advantage (Bürger, 1999). And no time would be lost nor risk involved in finding a mate. As all individuals produce offspring, the reproductive rate of the population would be at least double that of a sexual one of the same size with equal sex ratio. This indeed occurs in the hermaphroditic weevil *Otiorhynchus sulcatus* (Section **3.2.1.2**(**c**)). Such an advantage would often occur unless it could be defrayed by increased fertility in, say, long-lived sexuals (Waxman and Peck, 1999) or when males augment female fitness (Section **10.2.5.6**). So, why is sexual reproduction the rule?

The consensus, far from settled, is that sex generates variability; it can unlock *good genes from bad genotypes*. It promotes genetic variance, per se, to increase rapidly (Bürger, 1999), especially in changing environments (Waxman and Peck, 1999), and allows maintenance of directional selection (Gilbert *et al*., 2010). Genetic variability in a population is essential in such environments (Ford, 1975), permitting it to change and adapt (Fisher, 1930) and also to *spread risk* (Section **9.7**). Aphids (Section **5.3.1.2**(**h**)) are good examples. Temperate species often reproduce asexually in summer (benign conditions) and sexually before winter (variably harsh conditions). Fisher (1922), extending observations by Darwin (1859), pointed out that large populations have greater variability than small ones. Further variation results from the mating system. When individuals showing little genomic affinity mate it creates great variation. This is called *disassortative mating*, the converse, *assortative mating,* leads to less variability. In large populations the opportunities for disassortative mating are naturally greater. Of course, multiple mating (Section **10.2.5.6**) also generates more variable offspring. But this spectrum of *mate selection* must follow *mate recognition* (Section **9.8**).

9.7 Den Boer's Concept of Risk Spreading

Risk spreading, either spatially or temporally, concerns the strategies individuals employ relative to the unpredictable complexity of their future environments, and so is a subset of LHS. Thompson (1929) notes: 'Instinct … involves the disposition of things in relation to ends yet unknown, but no instinct … is able to arrange matters in regard to future events brought about through the play of pure chance'. 'Evolution is blind to the future' (Dawkins, 1989), risk spreading an individual's attempt to solve the dilemma of playing catch-up, namely the generation and maintenance of variability (Thoday, 1953; Waxman and Peck, 1999). Den Boer (1998) develops it as a theory of insect population, so we could include it with other theories (Section **11.2**). I consider it here more as an LHS, linking it to Southwood's theory in Section **11.2.2.5**: such strategies and population theory are interwoven. Risk spreading occurs at *both individual and population levels*. Individual actions in aggregate have population effects (Sections **9.6**, **10.1** and **10.2.4.1**). Conversely, risk to an individual can be estimated only from a study of population. We begin with the former, the focus of natural selection, and proceed to the latter. To repeat, risk spreading is an individual's response to an unpredictable future for its progeny. Were this not so close, adaptation would result from natural selection (Leather and Awmack, 1998; Hopper, 1999), rather as we have selected broiler fowls. Individuals can only generate variability and spread risk, as in classical financial investment. Den Boer (1968) does not develop individual aspects fully, but is well aware that selection acts on individual phenotypes: 'spreading of the risk … depends on selection of individuals' (p. 167), and in his 1998 paper refers at length to individual aspects.

While having other functions, egg distribution (Sections **9.1**, **10.2.4.7** and **10.2.5.2**) is a clear example of risk spreading. Diverse genotypes in a progeny spread risk; so does egg distribution, a behavioural trait that places phenotypes in different parts of the selective mosaic (Section **9.1**). Rarely, as in psychid and some lymantriid moths, does a female lay all the eggs in one batch. Batch layers usually deposit a higher proportion of the eggs than do species that lay eggs singly (Courtney, 1984; Section **10.2.5.1**). Achieved fecundity and risk spreading in space can be inversely related. Risk to eggs can be spread in space and time; however, for short-lived females these options are reduced. Temporal options are limited to the length of a female's reproductive life. At one extreme, in gall midges and mayflies, this extends to hours, not weeks or months. At the other extreme, adult dytiscid beetles (Section **8.2.2.4**(**b**)) may live several years. The options in space are also limited. Short-lived females cannot travel far: they must stay and lay. Even so, the strategy in *Tipula paludosa* (Section **3.2.1.2**(**f**)) illustrates the possible extent of their risk spreading. Emerging fully laden with eggs, they are too encumbered to fly. Most eggs are laid in their natal habitat, although not in one batch. On slimming down they fly and deposit the remainder elsewhere. All the eggs are laid at the about same time (within a day or two) and a majority, but not all, in the same area. The strategy works since the larval habitat, damp grassland, is extensive. But the female's power of seeking localized resources for the offspring is limited. Flying up, its light frame is swept off by even a light breeze. *Choristoneura* moths (Section **5.2.1.4.(c)**), which also inhabit extensive habitats, use similar tactics.

Long-lived females, as in several orthopteroids, have more options for risk spreading, commonly producing several batches of eggs that are laid at different times and places. Every week or so, according to weather, they produce a batch of ~20–30 eggs, enclose it in a protective ootheca, and place each parcelled batch at one of finally several points in their habitat. Risk is spread in time and space. Tachinid flies with microtype eggs may scatter >10,000 of them near their hosts (Section **8.2.2.5(h)**), their very number spreading risk. But many parasitoid wasps (Section **8.2.2.5**) face a dilemma of either laying an egg now or later, possibly in hosts that will give higher fitness (Rosenheim, 1999a). Other relatively long-lived insects with good powers of seeking larval resources are hawk moths (Section **5.2.1.4(i)**) and blow flies (Section **7.4.2.2**). Their options in time may extend several weeks and in space over many km^2, so that the majority of such an individual's progeny is protected from a local catastrophe. Migration itself evokes risk spreading on a wide spatial scale (den Boer, 1968), but has further outcomes (Section **12.1**). Cole's (1954) classic paper shows that natural selection favours a short life cycle with a single reproductive event (*semelparity*). That many species lay eggs over a long period in several batches (*iteroparity*) suggests that other drivers are at work, risk spreading being a likely candidate. Indeed, this strategy could be an adaptation to temporally unpredictable environments. Iteroparous insects usually feed during egg laying (income breeders), unlike most semelparous ones (capital breeders) that do not.

When there is dispersive polymorphism, the volant morph commonly takes longer to reach reproductive age than the flightless one (Zera and Denno, 1997) and is often, but not always, less fecund. Other risk-spreading tactics in time involve rates of development and diapause. In the cerambycid beetle *Steirastoma breve*, which girdles tree branches in Jamaica (Section **4.2.1.2(f)**), some of a brood within the same excised branch develop in 6 months and emerge for the next rainy season, while others take a year (Freeman, unpublished data). Similarly, often only *a proportion* of a population will enter diapause after breeding, as in Colorado beetles (Section **5.2.1.2(c)**), and only *a proportion* of a stage in diapause hatches or emerges. Therefore in the eggs of *Aedes aegypti* (Section **7.3.2.4(e)**) only some hatch upon first wetting, whereas others do so on subsequent wettings. In the tachinid fly *Bessa harveyi*, many adults emerge in spring, the remainder in autumn (Valovage and Kulman, 1986). The noctuid moth *Brachionycha nubeculosa*, which is local in Perthshire and Inverness, may remain in the pupa for 1, 2 or 3 years (South, 1920/1923; Ford, 1975). Similarly, the sawfly *Perga affinis* (Section **5.2.1.3(f)**) and the fruit fly *Rhagoletis pomonella* (Section **6.3.1.1(k)**) show a spread of emergence times extending over more than a year. Many other examples of risk spreading are given throughout this book.

Some aspects of risk spreading relate to what I call '*Fisher's Fork*'. Fisher (1930, Chapter 2) mused:

> It would be instructive to know not only by what physiological mechanism a just *apportionment* is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the *life history* and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction.

This is an early statement of LHS, a concept of wide generality, and my italics for emphasis. Often referred to as a 'trade-off' (Zera and Harshman, 2001). Indeed, we may further generalize Fisher's seminal query as, 'How and for what reasons are the metabolic resources of *an individual* allocated to its present and future requirements?' (Section **10.2.3.3**). A trade-off is a beneficial change in one trait causing a fitness cost in another trait (Stearns, 1992). Implicit here is that these resources are, indeed, *limited* (Section **2.4.2**; Mole, 1994); does a *real* trade-off exist? For risk spreading, this idea leads one to consider whether an organism should be semelparous, like a salmon or a gypsy moth, or iteroparous, like a cod fish or a locust. Birch (1960) says: 'The partitioning of energy between these various functions will be such as to maximize the chance for survival and multiplication' (i.e. RS). In semelparity, an individual allocates no resources towards continued survival, so maximizing them into reproduction. Iteroparous insects usually harvest food during egg laying, so increasing their stock. In two species of *Agonum* (Carabidae) survival and AF are reciprocally related (Murdoch, 1966a). While the spread of cold hardiness and fecundity in a brood could also be reciprocally distributed, metabolic resources can often be interconverted (Storey, 1990). Eggs can be reabsorbed and the antifreeze polyols diverted returned to glycogen. Individuals are not expected to accomplish both objectives at the same time, so that moths like *Operophtera* (Section **5.2.1.4(g)**) and *Eupsilia* (Section **10.2.4.2**), that lay eggs during winter, are food for thought. Fisher's Fork (forks originally had two prongs) can also apply to dispersive polymorphism, those dispersing often being less fecund (above, Section **12.3.3.2**; Zera and Denno, 1997; Simmons and Thomas, 2004).

The population consequences of risk spreading are stability, meaning the avoidance of extinction or at least increased persistence, especially because it operates at low densities where density-dependent processes are trivial (Milne, 1962). Added to such processes, individual and environmental variation dampen numerical oscillation inherent in populations (den Boer, 1968, 1998; Pimm, 1984; Łomniki, 1988; Grimm and Wissel, 1997). Higher levels of interaction, like the complex pressures from polyphagous predators and parasitoids and the interactions between them, will likely add further stability to our species (Nicholson, 1933; Elton, 1966; Benton *et al*., 2006). Even co-evolution between predatory and victim species *may* be stabilizing (Abrams, 2000). The impact of risk spreading should increase as communities become complex, so peaking in tropical rain forest. Here species diversity is high, while populations of most of them are sparse (Fig. 9.4a): *they persist at low densities*. By contrast, monocultured crops should show pest outbreaks (Elton, 1958; Pimentel, 1961; den Boer, 1968; but see van Emden and Williams, 1974). Risk spreading is positive feedback leading to progressively greater diversity, in turn offering greater persistence but lower densities for all the component species (Section **11.2.2.4**). It may even lead to sympatric speciation (Andrewartha and Birch, 1984; Section **9.10**). Such complex processes, however, are restrained in harsh environments.

9.8 Resources and Mates in Relation to Competition

Resources (Andrewartha and Browning, 1961) or *requisites* (Nicholson, 1933; Section **11.2.2.2**), of which food is the most significant, are items individuals need for continuing and/or improving their basic attributes of *growth, survival* and *reproduction*, and to fuel *movement* (Section **10.1**). As we have seen, their distribution determines the *potential distribution* of a species. In ecology, resources are *outside* the animal; *internal* metabolic resources must be so specified. Non-feeding adults, like crane flies and bot flies, live only a few days but avoid the conflicting needs of feeding and reproduction. Other insects lacking resources cannot be active for long and often pass any such periods in diapause. They have a *resource base*, which when biotic is lower in the food chain than they are. This base is influenced by physical and biotic factors, producing complex effects on the dynamics of a focal species. While exceptions exist, resources are usually contained in habitats (Section **9.5**) and vary in quality and quantity. They are *necessary, material and localized*. Oxygen, while vital, is ever present in terrestrial environments and so is not usefully considered as a resource. One exception would be juvenile *Mansonia* mosquitoes that probe sub-aquatic plants to respire (Section **7.3.2.4(c)**) – hence the oxygen contained therein *is* a resource. However, when the food resource is superabundant, as phytodetritus (Section **8.2.4**) may be, it may have less interest for autecology (Andrewartha and Birch, 1984).

Resources may be *physical* or, more usually, *biotic*; *consumable* (like food) or *non-consumable* (like spatial refuges; Section **9.9**); *temporary* or *permanent;* and usually localized. For temporary consumables the synchrony of their availability in relation to the needs of a species is basic to its dynamics (Bonal *et al*., 2010). For example, the beetles *Meligethes*, *Apion* and *Anthonomus* breed in ephemeral flowers. Some non-consumables, such as pupation sites, are usually always available, but others, like territories or nesting sites for solitary wasps, may be occupied only temporarily and then be unavailable to other conspecific adults. *Anthocharis cardamines* (Section **9.1**) often rests among the umbels of the ubiquitous cow parsley, *Anthriscus sylvestris*, against which its closed wings are highly cryptic, although its larvae eat other plants. It is a non-consumable resource and refuge, and *superabundant*. Resources may permit reproduction or just allow maintenance (Janzen, 1970), like flowering weeds providing nectar for wasps (van Emden and Williams, 1974). For reproduction, a group of associated resources constitutes a *resource patch* (Sections **9.12** and **12.2**).

Periods of resource finding (Section **10.2.4.7**) and discrimination precede resource use. The last activity is more critical if reproduction is involved. But the circumstances are diverse. A young larva may already find itself embedded in its food, as in insects infesting stored products, whereas a migrant aphid rarely lands on an appropriate food plant and despite an iterative search often fails to find it. Female parasitoids usually detect the habitat, then the patch or host's food plant, particularly if the host has eaten it, and finally assess host quality (Section **8.2.2.5**). Resources may become *absolutely* scarce as a result of a harsh physical environment or even because of competition for them (Andrewartha, 1970). More usually they are scarce *relative* to an insect's ability to find them. Section **10.2.4.1** examines the idea that adults of different species vary greatly in their ability to locate resources, especially those on wide spatial scales.

Food, the major consumable for animals, links the several trophic levels of organisms in a food chain, being the tangible form of energy and nutrient transfer. The biomass of succeeding levels, from primary producer to primary, secondary and subsequent levels of consumer, diminishes steadily at each step so determining the *pyramid* of numbers (Section **9.1**). There are two main reasons for this: (i) consumers rarely eat out the entire stock of food, often because they can find only a proportion of it; and (ii) biomass consumed is not converted with 100% efficiency. Models suggest that long food chains would be unstable (long return times after perturbation) for population dynamic reasons (Pimm and Lawton, 1977). The type of food defines an animal's *trophic niche* (e.g. herbivore, predator, parasite, detritivore), and in train a suite of integrated anatomical, physiological and behavioural characteristics. But trophic relationships are more complex than this linear chain suggests (Polis and Strong, 1996; Gange and Brown, 1997; Ohgushi, 2005, 2008), although the primary steps in this *cascade* of material can still be discerned (Hairston and Hairston, 1997).

Food may be living or dead. Its patchy distribution results from a range of natural forces *both physical and biotic*, which we will term *organic localization* (Section **10.1.2**). Organic patchiness is a special case of the more general process of *self-organization*, the emergence of order from disorder. In the mid-eighteenth century, the great French thinker Pierre Louis Maupertuis (Sections **9.10** and **11.1.2**) held that organic matter possesses self-organizing intelligence. But localization is a universal process (Prigogine, 1980; Kauffman, 1993; Rohani *et al*., 1997), both static and dynamic. A static, biotic example is the growth of a tree. A dynamic, physical case is the sorting of particles by size, in relation to current speed, during sedimentation in streams (Stokes law). This has consequent effects on the biota. A physico-biotic case is when wind-blown leaves collect in hollows, initiating patches of highly organic soil. Leaf litter driven by flooding during heavy rain may gather in a series of clumps or waves, leading to patchy soil fertility and resulting in a diversity of colonizing plants. The transport of such detritus between habitats is a critical feature of food web dynamics (Polis *et al*., 1997a, b). Then, vagaries of the wind often lead to discrete masses of flying insects (Pedgley, 1990; Burt and Pedgley, 1997; Section **10.2.4.5**), an important process for their dynamics. Such self-generating localizations, organic or not, can be regarded as *dissipative structures*, drawing energy into themselves, increasing in complexity, and finally senescing (McShea, 1998). Order may arise from order or from disorder, a duality noted by Schrödinger (1944). Host–parasitoid models may also show self-organizing dynamics (Comins *et al*., 1992).

The concept of *ecosystem engineering* is related to these ideas (Jones *et al*., 1994, 1997). Trees, by their continuing growth, alter the local ecosystem for many other species, although they may not provide food for them directly. For example, *Salix* spp. growing taller around a pond, shade it progressively, while their fallen leaves increase its acidity. This concept is, like so many recent examples, a development of one initiated by Andrewartha and Birch (1954), who give examples of both negative and positive effects between species outside the food chain (Section **10.1.2**).

Many differences exist between plant and animal food. Plants are primary producers or *autotrophs*. Excepting seeds and tumbleweeds, they are immobile, diversely defended (Section **2.4.2**), mainly carbohydrate, usually not very nutritious and variable in quality. They are often large relative to the consumer, and so may also provide favourable space for living and hiding (Section **9.9**). Herbivores rarely kill their food as predators do their prey, because (i) insect herbivores at least are usually specialized to eat only certain parts of it (Section **2.3.2**); and (ii) plants, unlike most animals, have great powers of regeneration after wounding. Prey are usually mobile and provide many relatively small, nutritious food items. For example, coccinellid and syrphine larvae kill and consume numerous aphids in a day, items that are rich in fat and protein.

Micropredators such as mosquitoes attacking relatively enormous tetrapod prey are exceptional, hence their special category (Section **7.3.2.4(c)**). In one way they operate more like herbivores: they consume very little of the food source without killing it. Conversely, their food is mobile, nutritious and not a primary producer. For many larval parasitoids (the *koinobionts*; Section **8.2.2.5**) and ectoparasitic insects on tetrapods (Section **7.1.1.1**), the food is relatively large and nutritious. They exploit their hosts not only as food, but also its strategies for survival. If their host dies of any cause, however, they may well die too. Ectoparasites also gain free heat from the high and constant temperature of their avian or mammalian hosts; feathers and hair conserve heat but also provide a warm and protected living space. Adult females of some parasitoids, such as *Melittobia* (Section **8.2.2.5(p)**), are small relative to their host and feed on it during the time they are ovipositing. They act rather like ectoparasites as well as being parasitoids. Of course, parasitoid wasps often feed on individual victims that they do *not* parasitize (Jervis and Kidd, 1986), reminding us that while we try to define things clearly, many systems have fuzzy edges because of life's extreme diversity.

Is dead food, such as litter, dung and corpses physical, biotic or what? Clements and Shelford (1939) regarded such material as separate from their biotic complex, but Allee *et al*. (1949) defined biotic factors inclusively. Andrewartha and Birch (1954) believe the distinction between physical and biotic to be 'unrealistic' and 'unsatisfactory', but while I agree with them on many issues I am with Allee on this one. Haeckel (1870) divided the environment into inorganic and organic (Section **9.6**). Chapman (1928) separated the physical from the biotic. Importantly, living entities (biotic) can behave and evolve, but once they are dead they cannot. And while Haeckel's definition is somewhat tangential, original definitions must not be forgotten. Science requires systematic building, not letting good, original concepts lapse (Paterson, 1982), only to be 'discovered' later, so achieving a hollow personal kudos. More like piracy than science. Lovell (1914) remarked smoothly 'A discovery in retrospect often offers little difficulty'.

First, food is indeed mainly organic, although having mineral components. Second, dead foods (cadavers, faeces, plant detritus) are products of living organisms. Their distribution, amount and nutritional value are related to the numbers and nature of the organisms that produced them, and of course to their rate of degradation and removal. Leaf litter nitrogen co-varies with that of the type of living foliage that formed it (Mattson, 1980b). Finally, several insects, such as strike fly maggots, feed on virtually the same food item whether it is living or recently dead, while earwigs, wireworms and leatherjackets are omnivores and feed on a wide variety of living and dead foods. But the fundamental ecological distinction is that *only living food can react to being consumed*, and possibly co-evolve with the consumer. Hence there can be true *interaction*. Dead food is merely depleted.

Food, like other resources, has quantity and quality. Quantity is often relative to an insect's ability to find it (Andrewartha and Birch, 1954; White, T.R.C., 1978). A single larva of the moth *Laothoe populi* on a poplar tree would have a superabundance of good food since these trees grow new, nutritious leaves throughout the summer. But a syrphine larva at the end of summer eating aphids when most had migrated would, in its blind wanderings, have difficulty in finding prey (Section **8.2.2.4(h)**). Quality describes the nutritive value of the food. Ecologically it can be regarded relative to its effect on an individual's RS. For plant food, nitrogen content is a rough index of quality, and adequate levels of essential amino acids and vitamins must be present. These are positive aspects of quality; negative aspects would be their lack plus the presence of specific defences and harmful secondary compounds (Section **2.4.2**). Quality varies with season, and for genetic and environmental reasons, within and between plant species (Orians and Jones, 2001).

Biological competition reached paradigm status long ago (Strong, 1980), while Dobzhansky (in Thompson, 1956) said it has emotional significance and should be eliminated from science. Not even Dobzhansky's advice has been taken. So, we must *define exactly* what we mean by it, what organisms may compete and what they may compete for. The myriad papers on competition remain obscure *without clear definitions*. Indeed, so much ire and confusion had been generated, despite attempts (Birch, 1957; Williamson, 1957) for clarity, that the Society for Experimental Biology held a symposium in 1961, which I attended as a somewhat awed research student, to discuss and define this thorny concept. First, empirical data must be separated from the results of simple models, namely *induction* from *deduction* (Section **11.5.1**). Then, *broad* and *narrow* definitions exist. The former is that *the existence of an individual constitutes a disadvantage to another at the same place so reducing its RS,* approximating to the *biotic* effects of selection. This broad sense is used by MacArthur (1972, p. 21), who fails to specify individuals. But the precise definition herein involves *a resource in short supply* (Dawkins, 1989), one *required by two or more individuals*, and called *resource competition*. Since quantity and quality are two aspects of a resource, competition can be for either or both aspects.

Competition is 'The action of competing or contending with others' (Anon, 1993), and 'The action of endeavouring to gain what another endeavours to gain at the same time' (Anon, 1980), this being closer to our concept. It implies co-occurrence. Milne's symposium definition has attracted many discriminating followers: 'Competition is the endeavour of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing when that supply is not sufficient for both (or all).' The 'thing' Milne spoke of is now termed a 'resource' (above). His definition is very different from Nicholson's broad concept (above; Section **11.2.2.2;** see Elton and Miller, 1954; Odum, 1971; Pianka, 1976; Thompson and Grime, 1988). My update on Milne is '*Resource competition is the endeavour of two individuals to obtain enough of a local resource when it is inadequate for one or both of them*', adding only *resource inadequacy* to the SOED's 1980 definition and implying quality.

Begon *et al.* (1996a and b) say competition is: '… an interaction between individuals, brought about by a shared requirement for a resource in limited supply, and leading to a reduction in survivorship, growth, and/or reproduction [RS] of the … individuals concerned'. This definition, and a similar one by Dempster and McLean (1998), extend Milne's and my definition by referring to the *negative results of the interaction*, *namely reduced RS*. But in our definition, *which is essentially behavioural*, detrimental effects may be trivial, moderate or severe. Either of two competitors for food or space may find an alternative supply so quickly that it is unaffected. Conversely, when two or more *Cephus* larvae compete in a wheat stem, only one survives (Section **4.4.1.1**(**b**)). Mutual confinement is an additional consideration. Also, competition should be more frequent at a high ratio of population(s) to resources, that is, density dependent (Section **10.2.3.7**). However, it is important ecologically only if there is a negative outcome. Indeed, Thomson (1980) refers to a *numerical response* in competition. But in accurate definitions, it is *individuals* who may compete, not populations (see 'methodological individualism' in Section **9.6**). Indeed, *only some individuals in a population*(s) may be competing, either in time or space (Connell, 1983; Andrewartha and Birch, 1984).

Keddy's (2001) definition is: 'The negative effects that one organism has upon another by consuming, or controlling access to, a resource that is limited in availability', again referring to short supply and reduced RS. Competition between plants is also resource based (Casper and Jackson, 1997). Birch (1957) defined a range of 'competitive' processes where organisms seeking a resource *that is not in short supply* none the less harm one or other in the process, which is too broad to be useful. For true competition in the field, a shortage must be *demonstrated* (Dempster and Pollard, 1981). But *potential* competitors do not always compete, indeed they may rarely do so (Lawton and Strong, 1981; Strong, personal communication). In summary, competition depends on population density, on localization of the interaction, on resource supply and to be useful must be defined to exclude other interactions within and between species (Thompson and Grime, 1988). Above all, it is *individuals* that may compete, *species* compete only as a consequence.

To back-track a little, competition, even in the broad sense, may take place only between members of the same trophic level. But many other interactions occur here, especially between heterospecific individuals and populations they comprise. *Resource competition* is but a subset of all possible interactions between individuals (Connell, 1983). As usual, too broad a definition fails to reveal the complexity of the ecological web. But some individuals, and so the species they comprise, are in a very broad sense more 'competitive' than others, an attribute compounded by abilities *in addition* to pure resource competition. These also include an ability to survive harsh *physical* conditions, to utilize a wide range of food efficiently and to combat enemies and pathogens effectively. In Thompson's terms, their 'specific intrinsic limitations' are less, so the populations they comprise are often more abundant. Rather than confound these abilities with broad competition, I term them '*ecological efficiency*' (q.v.). Fig. 10.13 shows that a wide range of tolerable temperature exists in different species, meaning that some individuals, and in train the populations and species they comprise, are more *ecologically efficient* than others.

Although resource competition may lead to reduced RS, this too must be shown (Lawton and Strong, 1981; Juliano, 1986; Finn and Gittings, 2003), not assumed. The strength of Milne's definition is that it allows one to *identify potential competitors, see if they compete* and then *test for negative effects on RS*. If an individual's RS is not reduced, competition is *trivial* (Section **10.2.3.10**). More usually it is reduced *significantly and to a variable extent*. Finally it *might be fatal* and hence cause direct mortality (Innocent *et al*., 2011), often reducing the RS of one individual, but resulting in zero RS for the other. Hence, when one party is affected more than the other, the negative outcome is *asymmetrical* (Lawton and Hassell, 1981). Population effects result from any or all of these categories.

Intraspecific competition, either between juveniles or adults, can have asymmetrical outcomes between the sexes. Small adult males resulting, say, from juvenile competition for food, may mate infrequently, small females are often less fecund (Southwood, 1978; Sokolovska *et al*., 2000; Berger *et al*., 2008). An odd situation, a result of competition between males for mates, occurs in polymorphic *Ischnura* damselflies. Females mimicking male coloration (blue andromorphs) when already mated are less harassed by males seeking mates than are normal brown variants. Copulating pairs are vulnerable to predation and harassment wastes time for oviposition. But blue females are disadvantaged at low density when unmated (Robertson, 1985; Cordero, 1992; Svensson *et al*., 2005). Similar effects occur in female *Papilio dardanus* in Tanzania (Cook *et al*., 1994) and in *Boloria eunomia* in Belgium (Turlure *et al*., 2016).

Generally, competitive success goes to the larger individual (Connell, 1983), and/or to the one who gets there first, called *pre-emptive competition* (Finn and Gittings, 2003; see Section **10.2.5.2** for 'Forrest's maxim'). Male *Centris dirrhoda* bees holding scent-marked territories attack other males that venture near, and usually win the contest (Raw, 1975). Competition is for territory. When butterflies such as *Anthocharis* (Section **9.1**) lay eggs the oviposition deterring pheromone (ODP) (Section **8.2.2.4**(**e**)) discourages egg laying by later females (Dempster, 1992). Competition is for oviposition site. In *Pieris sisymbrii,* red eggs act similarly (Shapiro, 1981). Red eggs are also found in *Pectinophora* (Section **6.2.1.2**(**g**)). But in the intense competition in the complex of ectoparasitoids confined within *Asphondylia* galls (Freeman and Geoghagen, 1989), the smaller, younger and later larvae have the advantage as lethal, external hyperparasites. Here competition is for the physical protection afforded by the gall, due to the adult, and the food provided initially by the midge larva.

Competing individuals may be conspecific or heterospecific, the outcomes being *intraspecific* and *interspecific competition*, respectively. In the former, genetic consequences are more likely (Section **10.1.2**). One may further distinguish sibling from non-sibling competition (van Alphen and Visser, 1990). In intraspecific interactions with a dead resource only the focal species is involved, but two are involved with a live resource, as the latter may well react to being consumed (Section **2.4.2**). In such competition several resources in common may be required, but this is less likely in interspecific competition. A further point involves inclusive fitness. Is it less harmful for an individual to lose competition to a relative rather than a non-relative, since the latter has no genes identical by descent with the former?

Odum (1971) calls interspecific competition where only one species is affected '*amensalism*', but *asymmetrical competition* is explicit (Connell, 1983). Here, two or three different species may be involved according to whether the resource is dead or living and so a reactive entity. The interaction is then *tritrophic* (Sections **1.5** and **9.1**). Thus, interaction of *Pemphigus betae* on the roots and *Hayhurstia atriplicis* on the leaves of *Chenopodium* (Moran and Whitham, 1990) shows asymmetrical effects mediated via the plant. While both aphids suck sap they never meet. Even so, *Hayhurstia* may suppress *Pemphigus*' numbers, but its impact is also influenced by the plant cultivar. *The resource is reactive and variable*. Again, when *Agriotes lineatus* (Elateridae) infests cotton roots it induces plant defences (terpenoids; Section **2.4.2**) that reduce the growth rate of *Spodoptera exigua* on foliage, often by >50% (Bezemer *et al*., 2003). Such effects may be modified by plant sectoriality (Section **2.3.2**). Environmental heterogeneity is a consideration when devising realistic models of competition (Section **11.5.2.2**) and in evaluating evolutionary outcomes. The fly *Pegohylemyia seneciella* does not oviposit in ragwort flower heads if larvae of the moth *Tyria jacobaeae* are already feeding on them (Crawley and Pattrasudhi, 1988), a case of *preemptive competition*. But the moth does not avoid flower heads invaded by the fly, again competition is asymmetrical. Even so, in the UK countless hectares of ragwort exist with no sign of either species! In the field one must look at the joint distributions of both (all) species (Hanski, 1983) and their mobility between sub-populations (Harrison, 1991; Cronin and Reeve, 2005). Also, interspecific interaction should be the more frequent form of competition in sparse species, that is, the majority (Section **9.4**), while in denser populations intraspecific effects would become increasingly pressing (Huxley, 1942; Pimentel, 1968). When a common resource is being used by two similar species, interspecific effects may exacerbate intraspecific ones (Connell, 1983), as in blow flies (Hanski, 1987; Richards *et al*., 2009) and burying beetles (Scott, 1998).

Such potential competitors may not compete in many places and/or for much of the time (Wiens, 1976; Connell, 1983; Walter *et al*., 1984). It depends on interspecific association (Cole, 1949). Then in a landscape, a good colonizer may co-exist with a good competitor (Skellam, 1951; Hanski, 1983). And while populations might be dense, food can be superabundant, as in phytodetritivores such as *Tipula* spp. (Coulson, 1959; Freeman, 1967b). But of course many species exist at low densities (Section **9.4**), with numbers being held down by other factors (Lawton and Strong, 1981; Murray, 1999; Section **11.2.2.4**). Indeed, enemy action can alter the outcome of interspecific competition. In some competing tropical ant species, the result is contingent on the role of their mutually parasitic fly *Pseudacteon* (Feener and Brown, 1997). This is best regarded as an aspect of trans-specific parasitism (see Section **10.2.3.9**). While interspecific competitors are sometimes confused as enemies, this approach clouds the issue: enemies and victims are not after the same resource! Then enemies *need* victims, but the members of no species *need* competition (Connell, 1980).

The two other facets of intraspecific and interspecific competition are: (i) s*cramble competition*, where individuals use up a resource but do not otherwise mutually interfere; and (ii) *contest competition*, where physical contest for the resource takes place (Nicholson, 1954; Hassell, 1975). Examples include: (i) *Pseudosphinx tetrio* larvae (Sphingidae) may eat out their food plant before maturing; and (ii) when several *Bactrocera oleae* larvae (Tephritidae) eat a single olive, some individuals form small pupae and others die. Females of the wasp *Sceliphron* fight at nesting sites (Freeman, 1977) and those of the ichneumon *Rhyssa* (Section **8.2.2.5(l)**) drive others from the same tree trunk (Spradbery, 1970). Apart from male *Centris*, in the solitary bee *Megachile apicalis*, females nesting adjacently are mutually aggressive, the larger often usurping the nests of the smaller (Kim, 1997), so here competition for a limited resource exists. But in *Sceliphron,* nesting sites *are not in short supply* so the interaction is *not resource competition*. Such intraspecific aggression may simply serve to limit local density and an attendant risk from enemies, and/or enhance reproductive output. Such aggression is often observed between enemies, both predatory and parasitoid, searching for their victims (Beddington, 1975). This may not be competition for resources, but rather spacing behaviour. Aggressive strategies, which may be evolutionary stable (ESS), are considered in racy prose by Dawkins (1989).

In the life cycle, one form of competition may follow another. In *Dendroctonus*, adult beetles contest for oviposition sites under pine bark, then the larger larvae scramble for space to develop (Reeve *et al*., 1995). In the butterfly *Anthocharis,* competition mediated via an ODP (above, Dempster, 1992) between females for preferred plants is followed on occasion by larval competition resulting in cannibalism (Courtney and Duggan, 1983). This also occurs in broods of burying beetles (Scott, 1998). Price (1984), following Park (1962), defined *interference competition* as 'any activity which limits access to a necessary resource' and *exploitation competition* as 'competition for a resource once access to it has been achieved and maintained'. Insightfully, P.W. Price (1997) regards competition as a *lateral effect*, as it occurs between members in the same trophic level (above; Section **10.1**). When larvae in high-density populations of *Tipula paludosa* attack, kill and eat each other (Section **3.2.1.2(f)**), it can be regarded as competition for space or better intraspecific predation. Normal food is abundant but cannibalism probably results in enhanced nutrition for the victor.

Our definition of competition is *precise* and *behavioural*, but it is still a broad term covering a variety of mechanisms. How do these impinge upon individual RS and so natural selection? In contests, larger individuals often have a physical advantage when in contact with smaller ones, as in the fundatrices of *Pemphigus betae* (Section **3.3.3.1(a)**) that hatch from single, relatively huge eggs (Whitham, 1980), and between larval *Aedes* (Juliano, 1998). Another probable example is between larval *Mesembrina* whose females lay very large eggs in cattle dung (Section **10.2.5.2**). Selection is ostensibly for big, competitive offspring. Pre-emptive, interspecific, interference competition occurs when cabbages massed with aphids deter cabbage root flies (Section **3.2.2.1(j)**) from ovipositing near them (Finch and Jones, 1989). Selection may be for early colonization, as in *Centris*. In scramble competition, fast-growing juveniles become larger females with higher fertility. Then, spatially and temporally rare competition, as in the *Tyria/Pegohylemyia* case, will not always cause selective changes in the species involved (Wright, 1975; Walter *et al*., 1984). Adaptation is not axiomatic each time a potential advantage is seen (Thompson, 1929; Williams, 1966; Gould and Lewontin, 1979). Due to pleiotropic effects, genes selected for competition may be otherwise deleterious (Wright, 1982a; Watt, 2000; Section **9.1**).

Continuing with resources, in considering reproduction in ecology and population dynamics, we are often concerned with fertility. Males may be regarded as a special type of resource for females, a reproductive resource. But we must consider genetic imperatives as these influence ecological processes. Both sexes pass on genes. Males may hold territories that contain food, as in some nymphalid butterflies (Baker, 1983), or simply provide mating space, as in *Centris* and some papilionid butterflies (Garraway *et al*., 2008). A territorial male may therefore be a proxy for favourable reproductive space and/or for ‘good’ genes, so affecting a female’s RS. Then, males may compete for females that have already found food. In *Onthophagus* dung beetles, males use their elaborate horns for access to and defence of tunnelling females (Emlen *et al*., 2005). Here sexual selection (Section **9.1**), rather than natural selection, is at work.

Eggs in most cases must be fertilized and so pass on genes from males. Females not only mate with conspecific males, but may try to choose ones that maximize their fitness. In *Melittobia,* the progeny from females mated with old males suffer ~50% mortality, compared to only ~25% for those mated with young ones (Freeman and Ittyeipe, 1993). Competition for such males, in turn, affects the outcome of competition among the progeny massed on the surface of the host, this being the main source of juvenile mortality. For males especially, the *number* of matings is critical genetically (Bateman, 1948; Trivers, 1972; Thornhill, 1976). As Burt (1995) puts it neatly: ‘The benefits of choosing well are likely to be modest compared to the benefits of being chosen often’. For females, multiple matings increase the genetic diversity of the progeny and may enhance AF (Ridley, 1988; Freeman and Ittyeipe, 1993; Oberhauser, 1997; Jennions and Petri, 2000). They typically seek better genes from new males (Yasui, 1997). Unsurprisingly, both sexes gain from promiscuity both in variability and numbers of progeny (Trivers, 1985, 2002). However, males often protect their genetic investment by displacing sperm from a previous copulation. For each species, a *specific mate recognition system* exists (Paterson, 1980, 1982; Walter, 2003), increasing the chance of finding a conspecific mate. This may be *augmented* to allow mate choice and operates through the spatial levels of the habitat (Section **12.2**), and comparable to other resource-seeking behaviours, herbivores for food plants and parasitoids for hosts (Section **10.2.4.5**).

Mates as reproductive resources are special, since the numbers of both sexes in a population normally vary together. Overall, the sex ratio usually remains constant, although not always 1:1 (Hamilton, 1967), irrespective of population density. Males in a brood often emerge before females, giving them better mating prospects, but causing a temporary imbalance in the ratio. This occurs in *Tipula luna* (see Fig. 4 in Freeman, 1964), *Opomyza florum* (Section **4.4.1.1(h)**), *Aedes punctor* (Packer and Corbet, 1989) and many butterflies: *Pieris* spp. (Shapiro, 1970), the white admiral (Pollard, 1979) and the bog fritillary (Petit *et al*., 2001). In *Rhagoletis pomonella* (Section **6.3.1.1(k)**), however, females emerge first, which may relate to their long maturation period. When females mate once only, the numbers of receptive ones decline rapidly during the season. Females often need to be mated without delay, which occurs when males are numerous (Fagerstrom and Wiklund, 1982). This also applies to females that mate several times. Asynchrony of emergence between the sexes as a result of habitat heterogeneity is reported in *Lymantria dispar* (Section **5.2.1.4(f)**). In sparse populations, this may exacerbate Allee effects, particularly on AF (Walter *et al.*, 2015; Section **10.2.2.3**).

When a progeny develops in mutual confinement its sex ratio is strongly female biased (*spanandrous*) (Hamilton, 1967). This is frequent in Hymenoptera (his Table 1). When the gregarious endoparasitoid *Tetrastichus howardi* emerge from lepidopteran pupae, ~94% of the progeny are female (Moore and Kfir, 1995, in Sullivan and Völkl, 1999). Even solitary wasps having viscous populations tend towards spanandry, thus the little *Pachodynerus* in Jamaica is 61.5 ± 4.7% female (Freeman and Jayasingh, 1975a). Hymenopteran females can determine the sex of the offspring and under such circumstances usually produce only enough sons to inseminate all the daughters. Spanandry is also found in thrips and scolytid beetles. In *Hypothenemus hampei* (Section **6.3.1.1(b)**), the sex ratio is typically ~9:1. But driving Y-chromosomes causing spanandry are known in some mosquitoes (Hamilton, 1967; Sweeny and Barr, 1978). Were they not restrained by other genomic mechanisms, they would result in the collapse of the affected population. Indeed, their use is being researched as a means of controlling these virulent pests (Curtis 1992; Hastings, 1994; Section **13.2.2.2**). Comparably, driving X-chromosomes are known in some *Drosophila* spp., causing various levels of spanandry (Burt and Trivers, 2006). Then the α-proteobacteria *Wolbachia* (Werren, 1997; Van Vugt *et al.*, 2009; Section **10.2.3.9**) and *Rickettsia* (Majerus and Hurst, 1997) can cause spanandry. Odd sex ratios sometimes occur. Broods may be all, or strongly biased, male or female, so promoting out-crossing. This happens in many gall midges and the semi-social bees *Eulaema terminata* (Bennett, 1965) and *Eu. nigrita* (Ackerman and Montalvo, 1985). The sex ratio in *Lymantria dispar* varies from female biased at low density to male biased at high-density (Myers *et al.*, 1998a and b). Naturally, such sex ratio variation has basic effects on population dynamics (Freeman, 1976, 1981c; Waage, 1982).

Competition for mates has parallels to that for material resources. Interference competition (Park, 1962) for mates covers all consexual interactions that *affect access* to them (threat, fighting, deception). Exploitation competition for mates includes any behaviour that *increases access* to them (advertising, mate sequestering – as in *Phloeosinus* beetles) but excludes consexual interaction (Wiley and Poston, 1996). While mates as resources have differences from other resources, insects seek them with comparable behaviours during appetitive movement (Section **10.2.4.1**). Specialized behaviours using visual and olfactory cues have evolved to promote conspecific mating (Parker, 1978; Paterson, 1980; Endler, 1992; Wickman and Rutowski, 1999), an event often occurring on the food patch. If not, leks may form in suitable places or males may hold territories, as in some *Centris* bees, the papilionid butterflies noted above and in some *Anastrepha* fruit flies. McLain (1991) explains that *r*-selected species, with short, chancy lifestyles, have little time for mate choice and hence sexual selection, their evolution being driven mainly by natural selection (Endler and McLellan, 1988). But in long-lived *K*-species, sexual selection acting similarly, which may well have different results, is more likely to operate. On a practical note, mate choice may confound the aims of SMT (Section **7.3.2.4(m)**).

To conclude, competition in populations relates to individuals, their distribution and density, and resource availability. We noted above some complexities of food and mates as resources, and any organism is a resource for several others: part of an interactive web (Andrewartha and Birch, 1984). The supply and quality of a resource can be viewed in relation to the logistic equation (Section **11.5.2.1, Eq. 11.2**) and to '*bottom-up*' effects on populations (White 1976, 1978; Hawkins, 1992; Section **10.1**). Very generally, competition is the *potentially* negative aspect of behavioural interaction within or between species at the same trophic level (Southwood and Comins, 1976; Rhoades, 1985; Price, 1997). While space too may be a resource, not all of it is usable by or useful to a given insect for growth, survival and reproduction. For additional aspects of competition as a biotic factor see Sections **10.12**, **10.2.3.7** and **10.2.3.10**.

9.9 Refuges and Danger Zones (Malentities, Hazards)

Throughout its life an individual insect runs through a *spectrum of risk*. Refuges relate to low, danger zones to high, mortal risk. Refuges may be spatial or temporal and so *places* or *times* in which the individual is partly or wholly free from destruction by inimical factors (Lawton, 1983), *be they physical or biotic*. Spatial refuges may result from the behavioural endeavours of the individual and/

or limit the searching efficiency of enemies. Danger zones are the opposite: places (Thompson, 1929) or periods where mortal risk is high. Both are useful concepts providing their meanings are not too attenuated. In sum, they refer to *environmental heterogeneity* (Levin, 1992; Jones *et al*., 1993).

A spatial refuge, being *material* and localized, can also be regarded as a *resource* (Section **9.8**), a component of the usable structure of an insect's world. But a temporal refuge *per se* cannot be a resource: it is not *material*. Spatial refuges, however, may have limited duration. Habitat space is often favourable in a general way as it contains resources in an accessible pattern and often a benign microclimate. A spatial refuge is more localized, providing partial or total protection from harsh microweather (Smith, 1935; den Boer, 1968), namely a *hygrothermal refuge*, and often from enemies, namely *enemy-free space* (Simmonds, 1948; Andrewartha and Birch, 1954; Nicholson, 1958; Atsatt, 1981; Jeffries and Lawton, 1984; Vet and Dicke, 1992). There is *predator-free space*, *parasitoid-free space* and *pathogen-free space*. The last named may be limited, but while their infective propagules are invasive they often need moisture. Spatial refuges can be diurnal, last for the duration of the instar and/or be seasonal or even permanent. Behaviourally they often deny information to enemies. Those for shelter are provided by *microtopography* or by *a plant's architecture*. Microtopography includes physical features such as banks, ditches, depressions, hillocks, rock faces and, remembering the small size of insects, even stones. But plant architecture (Lawton, 1983), both living and dead, is generally more important (Huston, 1994) and diverse, because the angiosperms, dominating the global land mass, have so many growth forms (Raunkaier, 1934; Takhtajan, 1969; Tiffany and Mazer, 1995). Plants often provide food resources and spatial refuges (Andrewartha and Birch, 1954; Lawton, 1983), ones that expand as plants grow. Of course, plants shelter many species, including endophytic pests such as root and stem borers, leaf miners, gall formers and fruit feeders, which live inside their food. Indeed, *Nepticula argyropeza* (Nepticulidae) continues mining in fallen leaves even when they are covered by snow (Hering, 1951). Microtopography and plant structure often modify the microclimate surrounding focal and other interacting species, and so influence their population dynamics (Monteith, 1960; Taffe and Ittyeipe, 1976; Freeman, 1981a; Mira and Bernays, 2002; Price *et al*., 2005; Karban *et al*., 2015; Section **10.1.1**).

Here are examples of spatial refuges. Early generation larvae of *Cydia molesta* (Section **6.3.1.1(h)**) bore peach twigs, where they may be parasitized by the wasp *Macrocentrus*. Later in the year they are protected in the deep refuge of the fruit. Similarly, larval *Anastrepha* and *Dacus* (Sections **6.3.1.1(l)** and **6.3.1.1(p)**) are often so protected. The wood-boring larvae of *Sirex* (Chrystal, 1928) and *Tremex* (Section **4.2.1.2(l)**) may be attacked by the ichneumons *Rhyssa* and *Megarhyssa*. But the ovipositors of these wasps, although long, cannot reach them in deep wood. Larvae below ovipositor depth are in an *absolute spatial refuge*. When the aphid *Sitobion avenae* feeds on wheat ears the younger instars seek situations deep between the developing grains, which partly protect them from the parasitoid *Aphidius rhopalosiphi* (Gardner and Dixon, 1985). And when *Diuraphis noxia* feeds on wheat the leaves curl and they move inside, again providing a *partial spatial refuge* from braconid parasitoids and coccinellid predators (Brewer and Elliott, 2004). The scale insect *Aonidiella aurantii* is less heavily parasitized by *Aphytis melinus* when on branches in the interior of citrus bushes than when more peripheral (Walde *et al*., 1989; Section **6.3.2.2(a)**). Larch sawfly (Section **5.2.1.3(e)**) larvae are less heavily parasitized by *Bessa harveyi* (Tachinidae) close to the ground than when a few metres above it (Monteith, 1960). Gypsy moth larvae often pupate in deep fissures in the bark of oak trees that provide a refuge, one augmented by their spinning a cocoon. While this involves a potential increase in population density (see Section **10.2.1**) it presumably results in better protection. In gypsy moth egg masses, the innermost eggs are protected from *Ooencyrtus* parasitism by the more superficial ones (Elkinton and Liebhold, 1990; Section **5.2.1.4(f)**), in effect a maternally constructed refuge. In Hokkaido, some of its egg masses are protected from avian predation during the depths of winter by being below the snow (Higashiura, 1989). In Alberta, Canada, *Ostrinia nubilalis* can have <10% larval mortality due to frost when they are under snow, but >90% when they are high in the maize stems (Lee, 1988; Section **4.4.1.1(d)**).

Apion dichroum (Section **6.2.1.2(a)**) fly from fields to adjacent woodlands in late summer and overwinter in leaf litter. But they are not randomly distributed there, having a tenfold greater density in the litter of hazel trees (*Corylus*) and beech litter under yew (*Taxus*) trees, than elsewhere (Freeman, 1965). The woodland is a *refuge habitat*, providing a less cold winter environment, the preferred litter forms *refuge patches* (Section **12.2**) giving further insulation. On a gross spatial scale the ladybirds *Brumus* and *Semiadalia* (Yakhontov, 1962) and some cutworm moths, all with specific refuge patches, overwinter in remote mountains. Appetitive movement (Section **10.2.4.1**) follows migration. Entomologists have long known of the existence of large spatial refuges, like marginal areas of rough grass, in which field pests overwinter. Formerly, their destruction as cultural control was employed. But such areas often provide refuges for their enemies (Section **13.2.4.7**), a factor also to be evaluated. We see that spatial refuges vary in scale. They can be pre-existing or constructed by the individual; often a combination of both. In a few cases they are maternally constructed, namely the cells of solitary wasps and dung beetles, and here food is provided, enemies discouraged and competition between sibling larvae prevented. So, the nests of social insects are communally constructed refuges.

The concept of a temporal refuge has been applied to asynchronous activity between victim and enemy: one is absent when the other is active. We look for diurnal and seasonal cases. Many caterpillars feed nocturnally, avoiding parasitoids and insectivorous birds that search during daylight. This strategy is often combined with a daytime spatial refuge, as in *Melipotis* (Sections **5.2.1.4(g)** and **10.1.2**). Crepuscular swarms of Nematocera occur in dim light in which they see each other but are almost invisible to avian predators (Land, 1997), although the latter may feed avidly at this time and dragonflies such as *Pachydiplax* cull such swarms (Section **8.2.2.3(a)**). Reduced desiccation may be a further factor. There are also cases of seasonal avoidance. Why do winter moths breed oddly in winter? Does it reduce predation on the adults, females being flightless, a partial seasonal refuge, or is the reduced duration of the egg stage compared to oviposition in the previous summer more critical, or what? *Phyllonorycter* species mine oak leaves late in summer, a habit avoiding interaction with a guild of spring-feeding caterpillars, including the winter moth, this being a temporal danger zone (West, 1985). But when reared artificially on spring foliage they do better than on late foliage, and hence normally would be afflicted by the tree's induced defences (Section **2.4.2**). These phenologies may be the outcome of several trade-offs, reflecting the lesser of several evils, but have been little studied (Remmel *et al*., 2009).

In many *Tipula* species (Coulson, 1959; Freeman, 1964, 1968; Freeman and Adams, 1972) and also in some mayflies (Corbet, 1964) and cicadas (Lloyd, 1984), there are mass emergencies and the period when the adults occur is short. In such cases satiation of predatory birds may lead to reduced individual risk for adults emerging close to the mode, while those emerging either early or late are at greater risk, as in *Tipula luna* (Freeman, 1964). For mayflies, Sweeney and Vannote (1982) show this effect of *inverse density-dependent* mortality (Sections **10.2.3.7** and **10.2.3.9**) on the mayfly *Dolania*, but point out that while mass emergence can satiate predators it may also facilitate mating. In a neat comparison, however, they found that three *parthenogenetic* mayflies had a similar synchrony of emergence, giving credence to the predator satiation hypothesis. Further, the resulting *normalizing selection*, illustrates Hamilton's (1971) 'temporal aspect of marginal predation'. Both spatial and temporal refuges have been covered in mathematical models and these predict not only stabilization of victim numbers, as one would guess intuitively, but also an increase in their equilibrium density (Section **11.2.2.2**), which one might not (Hawkins and Cornell, 1994; Godfray *et al*., 1994).

Danger zones are *places or periods* in which inimical factors are severe and localized, although space outside the habitat is generally one big danger zone. Tscharntke and Brandl (2004) call it 'the hostility of the environment', although '*hostility of the matrix*' would be better. The concept of 'hazard' (Thompson, 1924) or 'malentity' (Andrewartha and Birch, 1984) relates to our danger zone. The most obvious, tangible examples are places in which physical factors may prove fatal. My Colorado-beetle collecting swim off the coast of Brittany (Section **5.2.1.2(c)**) among thousands of these helpless brutes, the biblical records of locusts drowning in the Red Sea and the work of Cheng and Birch (1978, in Hardy and Cheng, 1986) on marine flotsam, illustrate the sea's hostile nature for insects. Although termite reproductives fly after rain, very many drown in the puddles. Indeed, water surfaces present a constant danger to numerous insects that have poor flight orientation. Diverse predatory insects (surface and sub-surface Heteroptera, flies such as *Hilaria* (Empididae) and *Poecilobothrus* (Dolichopodidae)) and also fish rely on such entrapment for their food. Arid regions too claim the lives of countless migrant insects unable to find water for rehydration, like *Anopheles pharoensis* migrating into the Western Desert (Section **7.3.2.4**(**c**)). Periods of enhanced danger, for example when insectivorous birds are feeding their nestlings (Remmel *et al*., 2009), also exist. Danger zones thus generalize the existence of peaks in the operation of a variety of both physical and biotic mortality factors; peaks in a range of risk. Again, refuges and danger zones refer to environmental heterogeneity in space and time.

9.10 Species and Speciation in Relation to Autecology

As a prelude we note briefly recent discussions of life itself (Vane-Wright, 2014). Animal life is marshalled into discrete, self-perpetuating entities that convert food into energy or their own substance. Unlike purely dissipative structures (q.v.), they produce, via epigenetics (q.v.) and other processes (Kauffman, 1993), order from order, but trophically order from disorder, reacting to the external environment to assist their own survival. Over time they respond to its heterogeneity by forming separate groups (species) which often remain distinct (speciation). But the view that the genome is the main driver of evolution (Fisher, 1930; Mayr, 1963) has been broadened (Haukioja, 1982) to embrace more fully the role of behaviour, a phenotypic product, including *ends-directed influences* (teleonomy), chance and necessity (Corning, 2014). Rather than genes driving individuals, individuals are said to employ genes for self-maintenance. If so, since genetic conflict exists (Burt and Trivers, 2006), one wonders why they do not keep them under better control. By what mechanism might they do so? Vane-Wright (personal communication, 2017) is developing the concept of 'integral evolution' as an explanatory framework. Haukioja argues that population genetics fails to explain several features of evolution, such as the emergence of longevity (but see Sections **9.7** and **10.2.4.1**).

Even so, since autecology is based on single species (Section **9.1**), species concepts are basic to it. In turn, speciation is relevant too, as it involves spatial distribution and population separation and remains an ever-present backdrop to autecological processes. Speciation, however, results not only in species formation but also engenders greater variability (Dobzhansky, 1940): more species, greater diversification and, ultimately, more complex interactions (below). And while species are human constructs we firmly expect them to have objective reality and duration (Coyne and Orr, 1998). Two probable causes for the continuing integrity of species are: (i) they are adapted to discontinuous ecological niches; and (ii) reproductive isolation creates gaps between taxa so allowing their independent evolution (Maynard Smith and Szathmáry, 1995). In a clear paper, Kirkpatrick and Ravigne (2002) discuss natural and sexual selection in speciation. In train, the process of *reinforcement* further separates allopatric species if they become sympatric later, selection acting against hybrids (Servedio and Noor, 2003). Species integrity may be long-standing. The staphylinid beetle genus *Micropeplus* has two fossil species dated 5.7 million years ago that are *morphologically* identical to extant ones (Coope, 1979). The caveat is that cryptic species may not be detected (Walter, 2003). Extensive studies of mosquitoes have revealed several complexes of sibling species (Section **1.4.4**, q.v.), as in the *Anopheles maculipennis*, *A. gambiae*, *A. quadrimaculatus* (Lanzaro *et al*., 1990, in Mallet, 1995) and *A. dirus* groups (Walton *et al*., 2001). We do not know if an enduring morpho-species is, in fact, a group of sibling species whose ecological features vary while their morphological ones do not. We expect closely related species to have evolved fairly recently from a common ancestor and have few genetic differences. But, as in British *Pilaria* (Section **12.3.4.4**(e)), they usually differ greatly in commonness and rarity. It seems that a few genes make or *reflect* big differences to their numbers.

Speciation also highlights the difference between *Linnaean species* (fixed, assumed to have been 'created'), and *biological species* (free to evolve; Mayr, 1942). As Darwin (1859) put it neatly, 'unity of type is explained by unity of descent'. But Linnaeus, unlike Darwin, did not travel widely, and perhaps was less aware that species may vary geographically. So we must consider the status of intermediate forms of biological species, either because of regional variation or because with time most species evolve.

Poulton (1904) suggested that successful interbreeding might be a helpful criterion to confirm species unity, but Mallet (1995) following Wallace (1865) points out that fertility and sterility often fail to distinguish species. In most species not all males and females are inter-fertile (with implications for RS), nor are all heterospecific ones always inter-sterile, and laboratory trials can be misleading. And as in our own species, copulation does not always lead to fertilization. While the criteria of reproductive isolation within the natural environment and of morphological difference work in most insects, there are several field examples of related species that are inter-fertile but retain their specific identity when sympatric or parapatric. Sometimes there are quasi-stable hybrid zones between parapatric species maintained by a balance between dispersal and selection (Barton and Hewitt, 1985; Virdee and Hewitt, 1994). Such zones are wider in species with greater flight capability. When starting ecological work on poorly studied insects one must anticipate the existence of regional variation, polymorphic forms and even sibling species (Section **1.4.3**), all with attendant ecological differences. More specifically, we expect the dynamics of their populations to exhibit regional variation, as Thompson and Parker (1928a) found in *Ostrinia nubilalis* (Section **4.4.1.1(d)** and Klug *et al.* (2008) showed recently in the leaf mining moth *Cameraria ohridella* (Section **12.3.4.1**).

Natural species comprise collections of populations, or demes, with considerable gene flow *within* them, less so *between* them. Speciation can occur by fragmentation and subsequent isolation of a panmictic population (*allopatric* speciation), by barriers to gene flow arising between two annectent populations (*parapatric* speciation, Wallace's classic mode), even by ecological separation *within* a population (*sympatric* speciation; Maynard Smith, 1966; Felsenstein, 1981; Wood and Keese, 1990; Via, 2001). Over long periods, faunal richness, migration excluded, depends on the balance between speciation and extinction rates. But because the global distributions of most species are greater than the typical redistributive distances of their members, opportunities arise for the generation and maintenance of extensive genetic differences (Gavrilets *et al*., 2000). Several features arising from speciation relate to autecology, particularly that natural selection is at its root a population dynamic process. So, we examine briefly the evolutionary process of speciation and then discuss some ecological outcomes.

To start, Darwin's major problem was not scientific. It was to educate a largely uncomprehending audience that species do indeed evolve into others (Huxley, 1942). Despite Maupertuis' promotion of evolution during the Enlightenment and Erasmus Darwin's support, Voltaire persuasively upheld the Christian notion of species fixity. Charles Darwin did not define speciation clearly in 'The Origin' (Turelli and Orr, 2000), but the view that species are labile fitted his agenda of the dynamic nature of evolution (Mallet, 1995). Then Wallace (1888) suggested that hybrids between two annectent subspecies could be ecologically inferior, although he had inklings of this principle much earlier. Assortative mating (Section **9.6**) would be favoured, leading to speciation. In the laboratory, this process has been shown to operate by removing hybrids formed between two closely related species of *Drosophila*, thus simulating maximal hybrid inferiority, and so promoting rapid speciation (Koopman, 1950; Thoday and Gibson, 1962).

Following Wallace, the traditional rationale of natural, parapatric speciation is as follows (Mayr, 1963). If two adjoining conspecific populations are subject to different selective forces, speciation can proceed when gene flow between them becomes reduced or absent. Like allopatric speciation it results from the independent evolution of geographically isolated populations (Barton, 2001). But in parapatric speciation, any *hybrids formed are disadvantaged* and multiple and diverse *barriers to gene flow* between the two groups develop (Wright, 1982a; Slatkin, 1985, 1987; Bush, 1994), reducing hybridization. Of course, only some individuals hybridize and the external environment is never constant. Such barriers may occur after fertilization (post-zygotic), may prevent fertilization (pre-zygotic) (Dobzhansky, 1970), or simply prevent copulation. Evolution should proceed to reduce genetic wastage, but a gene stopping fertilization between the two stocks could be favoured at any time. Generally, post-zygotic isolation results from the negative effects of epistasis realized only in the hybrids (Turelli and Orr, 2000; Burke and Arnold, 2001; Servedio and Noor, 2003). But this rationale has problems: isolating mechanisms have a selective advantage *only in the zone of overlap* (Dobzhansky, 1940; Moore, 1957). How then could genes selected for only in this zone spread to areas lacking mutual contact? Even so, in several taxa fixed zones containing unfit hybrids are known (Barton and Hewitt, 1985; Virdee and Hewitt, 1994). Speciation results ultimately in changes to the karyotype (White, M.J.D., 1978). In plants, but unusually in animals (Coyne and Orr, 2004), karyotypic changes themselves can cause speciation (Dobzhansky, 1940; Orr, 1996).

The South Australian morabine grasshoppers appear to provide such a case. Here White argues for chromosomal rearrangement causing speciation in the *vatica* group. In addition, Dover (1982) suggests that molecular drive (Section **13.2.2.2**) could lead to non-Mendelian evolution even to the extent of speciation.

Speciation often involves the *evolution of sterility*. Whether this evolves between individuals of incipient species, or sterile castes emerge within a species, a problem exists: how could *individuals with reduced or zero RS be selected for*? It is contrary to the basic tenet of reproductive advantage. The paradox gave Darwin sleepless nights (1859, Chapter 8), known as Darwin's 'special difficulty' (Costa, 2013). For speciation, Bateson (1909) offered a solution. The evolution of sterility could involve *two sets* of interacting genes. Only when mutant genes at two loci meet would bad effects ensue. Indeed, no reason exists why such effects should be limited to a two-locus system. Sterility does not evolve gradually, but suddenly when discordant genetic combinations meet for the first time. Dobzhansky (1937) showed this effect in two related *Drosophila* (*D. pseudoobscura* and *D. persimilis*), a result extended by Muller (1942), tested experimentally by Koopman (1950, above), shown recently by Servedio and Noor (2003) and called the Dobzhansky–Muller model (Coyne and Orr, 1998). Bateson is left out in the cold!

A feature of post-zygotic isolation is the universal *Haldane's rule*, the preferential sterility or inviability of hybrids of the heterogametic sex, whether male or female (Haldane, 1922; Orr, 1997; q.v.). For our purposes in population dynamics this is an acute loss of fitness due to genetic causes, but it also indicates that speciation by post-zygotic isolation may take place in a similar way in many types of animals.

Recently, species' definitions have been refined. A simple definition (Mettler *et al*., 1988, p. 21) is: 'The forms exist sympatrically or parapatrically in nature but maintain their distinctive characteristic; there is no cross-breeding or hybrid formation', which does not cover all cases (see above and below). Mallet (1995) questions the focus on isolating mechanisms, and suggests that advances in genetics should be incorporated in a *genotypic cluster definition*. This approach distinguishes 'groups of individuals that have few or no intermediates when in contact', and thus incorporates such an outcome 'as well as morphology'. Templeton's (2001) approach, after Simpson (1961), is also simple: if a species is not represented by a single evolutionary lineage, a historical perspective, then it is unified by considerable gene flow. This can be investigated by *nested clade analysis* (q.v.) of gene trees. Recall that Paterson (1982) and Walter (2003) (Section **9.8**) are also critical of the traditional concept of isolating mechanisms. In Paterson's *specific mate recognition* definition, reference to other species is unnecessary, but such recognition must work in the usual habitat. To my mind such a system, while maintaining species' integrity, grades into mate selection in general and in turn to enhanced or reduced RS and its dynamical consequences. Unfit hybrids may be significant in population dynamics because they are an intrinsic source of mortality (Sections **9.1** and **9.6**) and/or reduced AF. But hybridization between related species is far from unusual (Mallet, 2005). Although such species are genetically 'leaky', the rate at which they swap genes is insufficient to threaten species' integrity. While reinforcement and complete genetic isolation may take a long time, gene flow occurs at *ever-decreasing levels* during sympatric divergence (Berlocher and Feder, 2002). Sites and Marshall (2003) review methods for delimiting species. But are all species of the same type? Will a single definition cover them all? (Hull, 1997).

As expected, the separation of races, sub-species and species can be blurred. Recall that intense research may reveal, as in mosquitoes, the presence of cryptic species. Of course, races often develop in far distant parts of a species' distribution. But such a potential may exist even in adjacent habitats, as in *Tipula luteipennis* in the New Forest in England (see Fig. 1 in Freeman, 1968; Fig. 9.8). Here, peak numbers in a sphagnum bog were 3 weeks earlier than in a carr, only ~50 m distant. As usual in crane flies, adults were tenacious to their respective larval habitats. This is spatio-temporal isolation, but purely temporal isolation (*allochronic*) and speciation has occurred in periodic cicadas, a 17-year species giving rise to a 13-year one (Cooley *et al*., 2001). Sympatric speciation has long been suspected in the cichlid fishes of the East African great lakes (Turner and Burrows, 1995). Evidence that sympatric speciation in insects might often occur has been mounting (Gavrilets *et al*., 2000; Via, 2001; Berlocher and Feder, 2002; Prowell *et al*., 2004). But sympatry could simply depend on scale (Bolnick and Fitzpatrick, 2007). In a fine-grained environment, two different food plants might exist

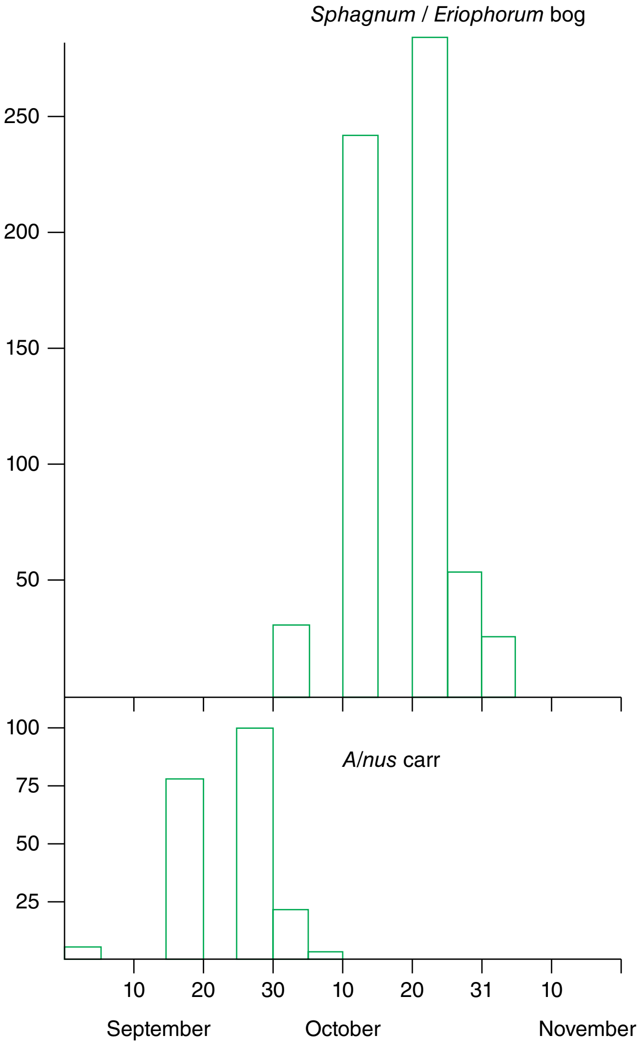


Fig. 9.8. The numbers of adult *Tipula luteipennis* sampled in two adjacent habitats. Adapted from Freeman, B.E. (1968) Studies on the ecology of adult Tipulidae (Diptera) in southern England. *Journal of Animal Ecology* 37, 339–362. Fig. 1.

in a habitat and lead to speciation within a given herbivorous species, as follows.

Long ago it was noticed that some oligophagous species oviposited more often on food plants they developed on rather than on those favoured by other conspecific females (Walsh, 1864, and Craighead, 1922, in Thompson and Parker, 1928b). In these early days, Lamarckian *inheritance of acquired characters* was mooted; latterly such behaviour is regarded as a potential path to sympatric speciation. The case is strong in some tephritid flies. In *Rhagoletis* (Bush, 1969, 1994; Smith, 1988; Filchak *et al*., 2000; Section **6.3.1.1(m)**), sympatric races have evolved in North America, one on apple, one on hawthorn and one on dogwood. In *Bactrocera cucurbitae*, there is a potential for sympatric speciation due to disruption of their complex mating rituals (Miyatake and Shimizu, 1999). While the inception of speciation in some *Rhagoletis* spp. is due to their choice of different food plants, interruption of gene flow must be shown (Jaenike, 1981), leading to natural selection for different phenologies (Smith, 1988). Further separation could arise, as above, from disruption of specific mating patterns (Hood *et al*., 2012). So, both natural and sexual selection would be involved. Also, when cryptic species are polymorphic, as in *Acleris* and *Achaea* moths (Section **10.2.3.5**), their proclivity to rest in matching but different parts of the habitat might lead to such speciation.

Our recognition of patches within habitats (Section **12.2**), namely habitat heterogeneity (Levin, 1992), provides an informative background to our understanding of sympatric speciation. Again, in the *Rhagoletis* complex, speciation of hosts may drive further speciation among their braconid parasitoids (Forbes *et al*., 2010). Note too that the ichneumonoids are very speciose (Section **8.2.2.5(k)**) even though many of them affect several host species. Complexity builds on complexity.

Similarly, *Acyrthosiphon pisum* (Section **5.3.1.2(h)**), in which different races feed on either lucerne or on red clover (Via, 2009; Via *et al*., 2000; Peccoud and Simon, 2010), shows reduced fitness of hybrids on the parental food plant. Even the parasitoid *Aphidius colemani* in searching for its host, *Myzus persicae*, has a preference for the plant cultivar on which its host had developed (van Emden *et al*., 2015). Such a reticulate process has been termed 'ecological speciation' (Schluter, 2001; Peccoud and Simon, 2010). Further, genetic correlations relating to the duration of development and the diurnal timing of mating, may also promote sympatric speciation (Miyatake and Shimizu, 1999).

Also note that for a given pair of species, the genes causing sexual isolation of males may well differ from those causing sexual isolation of females (Coyne and Orr, 1998). There is no reason why genes controlling male traits should be identical to those controlling a female's perception. Another probable case of sympatric speciation occurs in the membracid bug *Enchenopa binotata* complex (Wood and Keese, 1990). Here, populations on different food plants have different phenologies. But the development of *absolute* barriers to intergroup mating is unnecessary: divergence will occur as long as disruptive selection outweighs gene flow (Mallet, 1995). Diverse races of *Ostrinia nubilalis* exist in Europe, and have developed in North America since its arrival a century ago. Similarly, *Diabrotica* beetles (Section **5.2.1.2(d)**) have produced several North American subspecies. *Nilaparvata lugens* (Section **5.3.1.2(d)**), usually thought to be specific to *Oryza*, has a subspecies found on the related *Leersia*, which was separated from *Oryza* only recently. It seems that there are two sibling species of this plant hopper (Claridge *et al*., 1997). Overall, sympatric speciation may be uncommon because mating and recombination break down linkage dis-equilibrium rapidly, preventing the formation of genetically distinct sub-groups (Bolnick and Fitzpatrick, 2007). However, for population dynamics one must be mindful of the possible existence of cryptic species when conducting research. Following these possibilities for diversification we recall (Section **1.4**) Hutchinson's and Felsenstein's views on the numbers of living species.

We noted in Section **9.4** and above that some insect families contain far more species than others do. Large families, the product of long and intense speciation (Dobzhansky, 1940), tend to occur in endopterygotes and particularly in the Coleoptera, whereas small families tend to occur in the Apterygota and palaeopteroids. There are, however, numerous exceptions. Within the Coleoptera, for example, while the advanced Cerambycidae and Curculionidae are highly speciose, so is the more generalized Carabidae. But the advanced Meloidae contains relatively few species. I will not try to explain such irregular variation, merely to point out its existence.

10 The Principles of Insect Autecology 2: Innate Attributes and Environmental Factors

10.1 Introduction

Our classification of the relationships between the *innate, individual attributes of focal species* and the *external factors* they experience flows naturally from Haeckel's original definition of ecology (Section **9.6**). It concerns the science of *individuals in relation to their environment*, especially positive and negative outcomes on their *reproductive success* (*RS;* Section **12.3.1**) and refines the scheme of Andrewartha and Birch (1954). Cammell and Knight (1992) and Leather and Awmack (1998) have used related, but less comprehensive systems. Andrewartha (1970, p. 20) split an animal's environment into five components. Tauber and Tauber (1981) used a similar scheme for seasonal cycles. Berry (1985), examining a model of co-evolution, employed three species characteristics and five 'habitat properties'. Given natural complexity, it is critical to organize the 'species-specific relationships between individuals and the suite of physico-chemical and biotic aspects of the environment with which their survival and reproductive mechanisms interact' (Walter, 2003, p. 248). So the scheme here is not original, just more far-reaching than before, as required to improve our grasp of these relationships and in turn their application to biocontrol and integrated pest management (IPM) (Berryman, 1991b; Walter, 2003; Section **13.3**). The logical expansion of environmental factors is given in Fig. 10.1.

The *innate attributes* of a focal species (Section **9.1**) comprise *development, survival, movement* and *reproduction*. The interplay of these attributes of an individual with the nature of the environment determines its RS (Table 10.1), although the disruptive influence of chance always exists (below; Thompson, 1929). Then the interface of its responses to physico-chemical and biotic factors is expressed in its behaviour and physiology (Thompson, 1956; Maelzer, 1965; Krebs, 1972; Section **9.2**), responses often being sequential. Price *et al.* (2011) begin their extensive book on insect ecology with an appraisal of insect behaviour. Thus, the complex attribute '*reproduction*' involves maturation, mate finding, mate selection, fertilization, egg production, investment and distribution, all potentially interacting with environment. While our classification is clear-cut conceptually, it is less so in detail when we grapple with an intricate ecological web (Andrewartha and Birch, 1984), with multiple causes and effects (Mentis, 1988). But it does provide a framework that brings otherwise formless data to order. It is not a hypothesis, but elaborating Haeckel's definition, files data for later addition, comparison and refinement (Section **2.1**). Each action or interaction can be quite simple, but in aggregate they become complex, the variability of the individual and factor affecting each positive or negative outcome. Recall (Sections **9.1** and **9.6**) that individual variability has genetic and environmentally induced components, and that actions and interactions occur not only between the individual and environment, but also between factors and between attributes. What is more, evolution constantly promotes change (Haldane, 1954; Trivers, 1985).

Although environmental components are often regarded as *habitat properties* (Berry, 1985), in refining insect autecology these components are more stratified (patch, habitat, landscape) while properties of individuals must not be confounded with those of environment at any level. Thus, MacFadyen (1957) regarded a *niche* as a measure of environmental quality a species requires, and includes inputs from environment *and individual* (see Colinvaux, 1986, for a lucid discussion). So broad a concept is often applied in community analysis; in autecology it creates confusion. Similarly, the

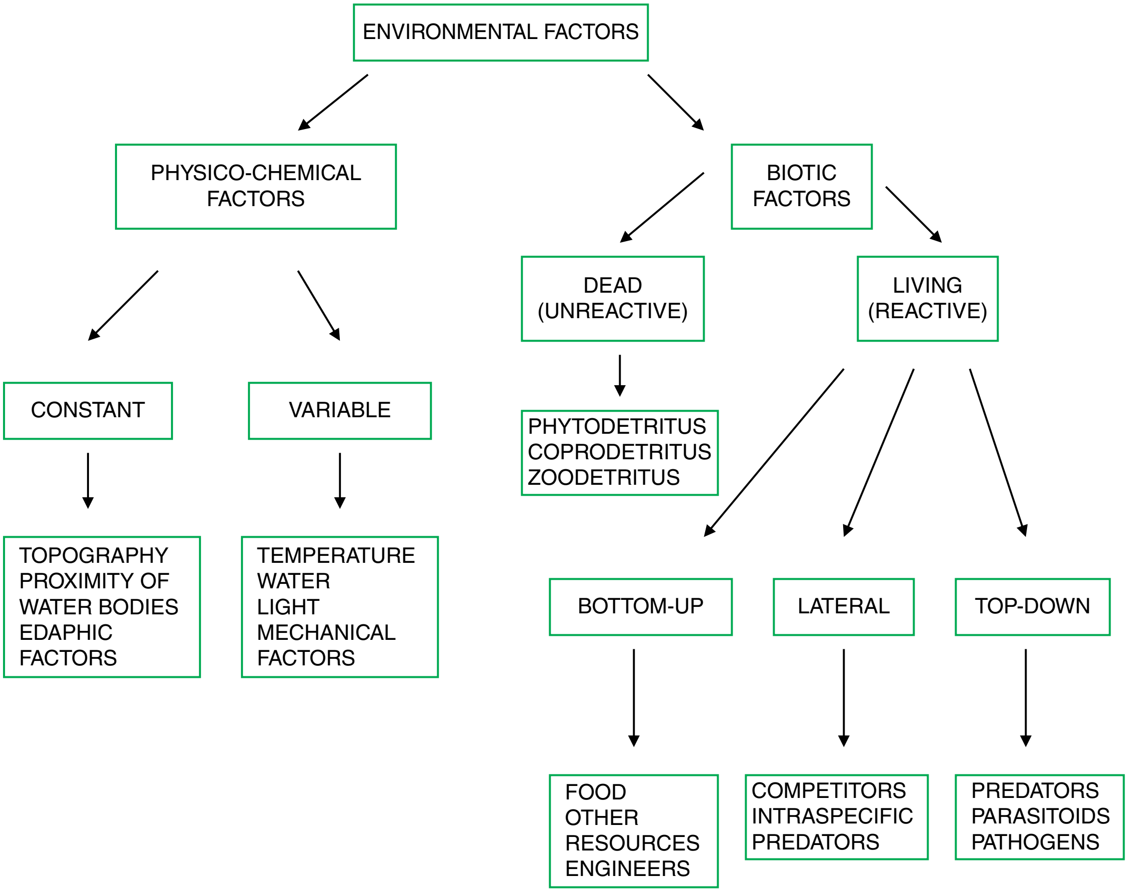


Fig. 10.1. An expanded scheme of environmental factors external to the organism.

Table 10.1. Suggested effects (+ or –) of environmental factors on the innate attributes of a focal species. Zero implies that the factor is not usefully considered.

	Physico-chemical factors					Biotic factors	
	Temperature	Water	Light	Mechanical	chemical	Conspecific	Heterospecific
Growth	+/–	+/–	0	0	+/–	+/–	+/–
Survival	+/–	+/–	+/–	+/–	+/–	+/–	+/–
Movement	+/–	+/–	+	+/–	+/–	+/–	–
Reproduction	+/–	+/–	+	+/–	+/–	+/–	–

Note: Most physico-chemical factors have positive or negative effects on individuals due to whether they are optimal or extreme. Conspecific effects relate to population density. Non-conspecific effects are generally negative, being due to enemies, less commonly they are positive (good food and mutualists).

age of an individual when it is invulnerable to an enemy, cannot be confounded with a refuge (Section **9.9**). Nor in assessing landscape connectivity (Tischendorf and Fahrig, 2000) can an insect's ability to redistribute be confounded with landscape properties. Different individuals and species have diverse innate abilities to migrate, disperse or seek resources (i.e. individual searching capability, ISC; Section **10.2.4.1**), which only in turn are influenced by the characteristics of habitat or matrix.

There are contemporary *actions* (e.g. a Colorado beetle freezes to death) and contemporary *interactions* (e.g. two *Papilio* males contest a territory). Physico-chemical factors often have an *action* or *influence;* biotic ones normally involve *interaction*. The former factors often act in sequence. A daytime increase in insolation on the ground causes greater evaporation and later showers may fall. Biotically, an increase in a female's mass due to past good food may lead to her present high fecundity. But it can be hard to separate a one-way *influence* from a two-way *interaction*. Does one larva feeding on a big tree induce any negative action (hence *inter*action) on that *tree*? It does, but it is trivial. At the level of a twig, however, it might have, as defensive compounds may be released. What can be important at the micro-level may be trivial at the macro-level.

Then there are *trophic interactions* (herbivory, predation), less often *non-trophic interactions and influences* (competition for space, environmental engineering (below), signalling). Weather often alters the *direct interaction* between individuals of two species, as in predation and competition (Burnett, 1949; Atwal and Sethi, 1963; Connell, 1983), or by those of a third species (Freeman, 1974, 1977; Wootton, 1994; Wootton and Emmerson, 2005), the action being *indirect* (Thompson, 1929). Examples of cases of physical factors affecting biotic ones include: (i) low temperature may limit the capacity of parasitoids to search for hosts, as in the aphidiine enemies of aphids (Section **8.2.2.5(m)**); and (ii) harsh weather may kill early instars so that intraspecific competition in later ones becomes trivial, as in *Tipula paludosa* (Section **3.2.1.2(f)**). While Markovian processes (q.v.) are often applied to behavioural sequences (Section **10.2.4.1**), called reaction chains in ethology (Eibl-Eibesfeldt, 1970), they may well have analytical value in the present context.

But correlation is not causation (Cole, 1958; Jackson and Somers, 1991), while causes may not operate simply in a linear way. Then, nonsense correlations often exist between unrelated variables. So where in a causal sequence does our interest centre? Thomas Aquinas (Section **2.1**) was naturally engrossed in the Ultimate Cause, but we Earth-bound ecologists may regard proximate causes of greater interest. Indeed, *only proximate causes of mortality are entered into life tables* (Section **11.4.2**). While regional insect diversity correlates with regional insolation (Turner, J.R.G. *et al*., 1987) and butterfly numbers relate to the North Atlantic Oscillation (Westgarth-Smith *et al*., 2005), more proximate mechanisms, such as insects laying no eggs below a threshold temperature, is of more practical use. In considering the regulation of insect numbers (**Chapter 11**), the sequential operation of external factors must always be borne in mind. As we have seen, physical factors often *legislate* biotic ones (Nicholson, 1933). Then, our set of conceptual pigeonholes provides research direction and is valuable for learning the subject. New information, often from different sources (i.e. pure and applied ones), can be filed appropriately, leading to new comparisons, to an improved classification and, ultimately, to hypotheses. Facts do not create science spontaneously, they must be 'interpreted and thus embodied in an intelligible synthesis' (Thompson and Parker, 1927). Classification is our assistant.

Innate attributes then, *compound to give individual or in aggregate populations, RS. Physico-chemical* factors such as temperature, moisture, light, environmental chemicals, soil pH, diverse mechanical events, or *biotic* ones like population density (a conspecific effect), enemies, mutualists and food (usually heterospecific effects), influence these attributes. The term 'abiotic' is often used as short hand for the former factors, but tells us what they are not, rather than what they are. On a gross scale, Drake *et al*. (1995) regard the *invariant physical features of the landscape*, like topography and the proximity of water masses, as separate from *variable factors* such as local weather. Simply, physico-chemical factors are either *constant* or *variable* (Fig. 10.1). This is established practice in pedology (White, 2006) and essential in unravelling global dynamics (Section **12.3.4**). Topography influences nutrient transfer in streams and run-offs (Raghu *et al*., 2013) and insect redistribution via landscape connectivity (Goodwin and Fahrig, 2002). It can be explanatory when investigating insect dynamics at larger spatial scales (Weiss *et al*., 1988). Wellington (1954) stressed the importance of continental weather systems (global) on insect ecology. But on a landscape scale, he gives a graph (Fig. 7 in Wellingon, 1964) of how the effects of cloudy and rainy days differ between a valley and an adjacent hill. Indeed, hilly regions embrace a variety of habitats (Pianka, 1966), much being due to soil diversity. Even on small scales (1–10 ha), sloping terrain and gullies direct rain water to lower areas which stay moist and nutrient rich, enhancing organic diversity. The nature of the soil, a further effectively constant factor, also affects water retention. Slope and aspect have additional effects. *Topographical complexity promotes species diversity*. Such complexity may interact with annual changes in weather allowing population persistence (Weiss *et al*., 1988). In dry years, wetter parts of the landscape may favour our species, and vice versa in wet years, tending to promote numerical stability. But topographical diversity in landscapes can also drive a spread of emergence times (Freeman, 1968), result in asynchrony in mating opportunities and fewer females being fertilized (Walter *et al*., 2015). On decreasing spatial scales we have the sequence:

Sun/Earth → Global → Landscape → Habitat →
Physico-chemical → Biotic → Individual

This simplified scheme, omitting for example biome, matrix (Section **9.3**) and patch (Section **12.2**), ranges from the solar system to the individual. Physical factors impinge on an insect within its own living space, but form a chain of events reaching back to the Earth's solar environment, events that often override biotic ones.

Then one must bear in mind the less tangible and largely temporal effects of physical *predictability and uncertainty* (Stearns, 1981): the former again being due to the inexorable motions of the Sun and Earth (Section **2.2.2**). Far from the tropics the arrival of winter is certain, but its timing and severity are not. Biotically, on a micro-scale, the *probability* of finding a host is a major determinant of how many parasitoid species attack it (Askew and Shaw, 1986). Host duration is a related factor. In nature chance is always a player (Thompson, 1929; Holling, 1973; Benton *et al*., 2006). Uncertainty is sometimes modelled in population processes (Turchin, 2003) and even weather, which is rarely modelled, is driven partly by chance components (Rind, 1999; Section **2.1**). Then in bark beetle ecology, if a pine tree is *by chance* close to a previous attack it is more likely to be overwhelmed (see Table 7 in Raffa and Berryman, 1987). Chaos has also been implicated (Vandermeer, 1982; Lewin, 1993; Ellner and Turchin, 1995; Zimmer, 1999), but means different things to different people (see Section **11.3**).

For animals at least, gross physical factors, originating as components of weather, are unaffected by the focal species on which they act. While other species may modify their impact, there is no measurable feedback, no *inter*action. So they are termed *exogenous factors* (cf. Nicholson's *legislative factors*, Section **11.2.2.2**). But biotic factors, especially living organisms truly interacting with the focal species, are *endogenous factors* (cf. Nicholson's *governing factors*). There is feedback and a potential for population regulation, co-evolution and change (Section **8.2.1**). Biotic factors operate from lower in the food chain (*bottom-up, resources*), at the same trophic level (*lateral effects, competitors*), or from higher up (*top-down, enemies*) (Table 10.2; Mattson and Addy, 1975; Hunter *et al*., 1997; White, 2001; Moreau *et al*., 2006). This scheme, arising from synecology, is usually applied to herbivores, but of course, it is valid for predators as their RS is also affected by food and enemies.

Bottom-up and top-down factors may be linked, as when caterpillars use defensive chemicals from plants to deter enemies (Dyer, 1995), making another strand in the ecological web. While this scheme omits physical factors, these have strong, modifying effects and so become incorporated as ultimate factors, called indirect factors of Thompson (1929) (below). While we have classified environmental chemicals with physical factors they often arise from organisms. Complex pheromones alter the intraspecific environment. Some flowers in the Araceae produce heat and mammals respire CO_2 which biting flies detect. Indeed, both insects and plants produce volatile organics and rotting plants produce acids. These compounds affect insect behaviour in three ways: they may be repellents, attractants or arrestants; physiologically they may be poisons.

Table 10.2. A Classification of biotic interactions.

Conspecific	Lateral	Bottom-up	Top-down
Competition	Competition	Herbivory/ plant defence	Predation/ defence and avoidance
Co-operation	Effects mediated via[a] planta	Detritus feeding/no defence	Parasitism/ defence and avoidance
Mate finding and selection		Symbiosis/ mutual benefit	Disease/ defence

Note: The table assumes that the focal insect species is either a herbivore or a detritivore. When a carnivore or a parasitoid its victim's defence and avoidance are bottom up effects, the focal insect being subject to top-down influences such as avian predation.

[a] The lateral effects of competition are often mediated in this way.

But with biotic factors it may be hard to discover who is in the driving seat (Myers, 1980; Fig. 10.2). Are herbivore numbers limited by food from below or by enemies from above (Hawkins, 1992)? Enemy numbers could be driven by the availability of their victims, a point made by Thompson (1929), for the parasitoid *Eurytoma* attacking gall flies by Varley (1941) and for parasitoids of larch budmoths (Baltensweiler and Fischlin, 1988). Even so, there is a strong case that parasitoids drive the cycles of some forest pests (Berryman, 1996). The extensive outbreaks of the leaf miner *Cameraria* in Europe, freed from its original parasitoids (Klug *et al.*, 2008), may be a recent example. The many successes in biocontrol also argue for the reality of top-down effects on herbivores (Sections **12.3.2.3** and **13.2.4.6**), while enemies do indeed cause the greater part of their juvenile mortality (Cornell and Hawkins, 1995; Section **11.4.4.1**). And we expect complexity not simplicity.

In the biotic complex the *population density of the focal species itself* must be singled out. Unlike other factors, it is intrinsic to and inseparable from the population on which it acts (MacArthur and Wilson, 1967). Darwin (1859, Chap. 3) touched on this: '... there must in every case be a struggle for existence, either one individual with another of the same species, or with individuals of distinct species ...'. The spacing of conspecific individuals affects each of them. This spacing (density) acts as the ultimate self-regulator (Milne, 1957b). It has *primary effects* such as: (i) dis-operation and co-operation (intraspecific competition and facilitation; Southwood and Comins, 1976); (ii) on emigration (Section **10.2.4.6**); and (iii) on mating frequency (Section **10.2.5.6**). *Secondary effects* are due largely to its influence on the action of enemies (Sections **9.4** and **10.1.2**).

Fig. 10.2. Professor Judith Myers, prominent among a recent group of women who are making significant and welcome advances in insect ecology. Reproduced with kind permission from Professor Myers.

To amplify: while physical factors may act on individuals directly, either singly or in combination, they may also act as *ultimate factors* in a causal chain, recalling the *direct* and *indirect* interrelations of Thompson (1929) and Maelzer (1965), with biotic factors having more *proximate* roles (Section **12.3.4.3**). When the latter are enemies or interspecific competitors (Section **9.8**), physical factors also influence their growth, survival and reproduction, just as they do the focal species, but often in different patterns, especially for vertebrate predators. Biotic factors often act in a chain among themselves (e.g. plant, herbivore, carnivore, parasitoid, parasite) and complex interactions between them are frequent (Andrewartha and Birch, 1954, 1984; Thompson, 1956; Freeman, 1973a, 1982; Freeman and Parnell, 1973; Holt, 1984; Wootton, 1994; Ohgushi, 2005). Both sets of factors are distributed in time and space (Section **2.1**), time being primarily diurnal, sometimes lunar, annual or of longer periodicity (Section **2.2.2.1**), and space being variously stratified (Levin, 1992; Sections **9.5** and **12.2**). For a herbivorous insect and its enemies there may be the following chain of actions and interactions:

Physical Factors (temperature, water, light) →
Food Plant (species, age, season) →
Food Quality (nutrients, sugars,
amino acids, their spectrum, concentration,
secondary compounds) ↔ Focal Herbivore
(nutritional status, size) ↔ Enemies (predators,
parasitoids, pathogens)

Although we try to extract the various components of the insect's environment for analysis of their influences, in reality they often act in concert, producing great complexity, while the individuals on which they act vary.

Insects and other organisms emit, purposefully or accidentally, physico-chemical information, and detect and process what they receive with an array of sensory organ systems (Altner *et al*., 1981; Wigglesworth, 1984; Endler, 1992; Hildebrand, 1995). For example, there are six types of sensilla on the antennal flagellum of honey bees, while male *Manduca sexta* (Section **5.2.1.4(i)**) have ~300,000 olfactory receptor cells on this organ, ~40% of which respond only to pheromone blends from females (Hildebrand, 1995). Generally, insects detect chemicals, light, temperature, humidity and vibration, the first two being the most important for their informational content. Environmental compounds, from simple ones like CO_2 (Bowen, 1991; Dekker *et al*., 2005; Guerenstein and Hildebrand, 2008) to complex organics like ecomones, are often produced by organisms. They may be airborne, on surfaces (Noldus *et al*., 1991, in Vet and Dicke, 1992) and in food. Olfaction processes the former and gustation the others. Chemical *patterns* are signals from other organisms (Witzgall *et al*., 2008) carrying information. Perception is a *subjective filter* that processes *objective reality* (Schaefer and Ruxton, 2009).

Insects are sensitive to the presence, intensity, colour and periodicity of light. But their vision, the *perception of spatial pattern* (Prokopy and Owens, 1983) and its *recognition*, can be well developed. Vision is far more complex than mere photoreception, as is olfaction from gustation. Signals from other organisms are modified by environment. Thus, the greenish light in a forest affects perception therein of colour patterns. If an insect is in the right *physiological* state, after neural processing, sensory inputs initiate *behaviours* having *ecological* outcomes. While insects perceive physical factors directly, they recognize biotic ones such as food, enemies and conspecific individuals by detecting them indirectly via vision, smell, gustation and vibration, their behaviour being conditioned by sensory input, integration and learning (Papaj and Lewis, 1993; Gumbert, 2000). To initiate appropriate behaviour they must recognize incoming signals, whether from physical or biotic sources. For the latter, whether or not an organism is conspecific is of primary importance. Thus, a *specific recognition system* exists of which a *specific mate recognition system* (SMRS) is a component, one vital to reproduction and reproductive isolation (Paterson, 1980, 1982). Enemies must be recognized if defences are to be deployed. But the identification of any object implies that an innate pattern exists in the memory with which the received pattern can be compared. Recognition is an essential part of behaviour. The way in which learning improves upon innate recognition is discussed brilliantly by Lorenz (1965).

But perception is imperfect, reducing with background noise and distance, and the output of information from organisms is often false: there is *natural deception* (Hinton, 1973; Trivers, 1985, 2011). We deal with *visual deception* in Section **10.2.3.5**, but *chemical deception* of body surfaces is also very common (**Chapter 8**), possibly more common, at least for insects, and *works in the dark*. Thus, ants are deceived by aphidiine parasitoids of aphids (Völkl, 1992; Dettner and Leipert, 1994; Liepert and Dettner, 1996) and by inquilines and parasitoids in their nests. *Bombus* workers are deceived, both visually and chemically, by the parasitic syrphid fly *Volucella pelucens* (Colyer and Hammond, 1951) and by parasitic *Psithyrus* bees (Section **8.2.2.5(z)**). Chemical deception even extends to the case of parasitoids injecting specific venoms into the neural system of their victims, so modifying their behaviour to the aggressor's advantage (Libersat *et al*., 2009). Plants also use chemical deception, altering the behaviour of insects. For example, the wild potato, *Solanum berthaultii*, has glandular hairs producing (E)-β-farnesene, the main component of aphid alarm pheromone. This causes *Myzus persicae* to disperse (Gibson and Pickett, 1983). Indeed, chemical deception is commonplace at the molecular level.

These are the elements of insect autecology, systematically exploring the relationships of individuals to their environment. While some aspects are behavioural and/or belong to environmental physiology (Wigglesworth, 1984; Danks, 2007), the effects are broader in scope. Thus, *the mechanisms that buffer the individual against the vagaries of its environment, in aggregate buffer the dynamics of the population of which it is a member*. These mechanisms may be *structural*, like the tough integument protecting most beetles against invertebrate predators, *physiological*, such as ionic regulation and cold hardiness, or *behavioural*, such as the ability to seek favourable microenvironments and refuges (Section **9.9**). Indeed, *behaviour and physiology often comprise a sequential buffer zone, between environment and individual, mitigating dire ecological outcomes*. Mobile stages can move away from physical extremes, while in train their physiology may be attuned to resist them, as in diapause (Section **10.2.3**). We recall (Section **1.3**) that eggs and endopterygote pupae are largely debarred behavioural defences. Some herbivorous insects, like *Pieris rapae*, eat more food when it is poor (Moran and Hamilton, 1980; Slansky and Rodriguez, 1987; Danks, 2007), thus substituting quantity for quality, a strategy also found in some birds feeding their young (Wright *et al.*, 1998). While *r*-selected insects (Section **9.1**) like aphids have defences, they are best developed in *K*-selected and long-lived species (Vallin *et al.*, 2005). Individuals are not merely passive actors in this ecological play, but respond to mitigate inimical conditions (Endler, 1992) and react to favourable ones, this having population effects (Freeman, 1974; Wootton, 1994; Ohgushi, 2005).

But these elements give us an incomplete explanation of how and why the density of the focal species varies spatio-temporally, as they tend to be deficient in time-dependent processes (Section **11.2.1**). They tell us, however, why our species cannot exist outside certain places or cannot be active at certain times (Cook, 1924; McDonogh, 1939; Freeman, 1977, 1981a; Thomas, 1983; Gevrey and Worner, 2006; Section **12.3.4.3**). They affect growth, survival, redistribution and natality: the building blocks of population dynamics and must be weighted and integrated in our enquiries. Some factors are critical for a focal species and situations while others are not, which the ecologist must judge. But since they influence its birth and death rates (RS), and those of its enemies and competitors, they should enter into equations of population change (Section **11.5**) and help us assess the latter's verity. While models aim to simplify, to discover the essence of *population processes* (Section **12.3**), I aim here to expose their underlying complexity, an aim requiring precise definitions (Hansson, 2003). In all, these interactions reveal a potential range of phenomena to investigate, the results of which underpin the analysis of population processes, both time dependent and time independent (Section **11.4.3**).

Harsh physical factors, like extremes of cold and aridity, delimit the distribution of species in time and space, so one might think of them as *limiting factors*. The concept derives from von Liebig in about 1850 who discovered that lack of phosphorus could limit plant growth (Colinvaux, 1986). The idea was that an essential substance needed in only small amounts could act like this. But Elton (1927) used the term to imply that a given species is sensitive to *only one or two* environmental factors, while Thompson and Parker (1928a) used it for factors that reduced the efficiency of parasitoids. Following Andrewartha and Birch (1954) and Dixon *et al.* (2009), however, the following is preferable. With *hygrothermal factors* there are *favourable ranges* within which the focal species lives 'normally': namely its activities of searching, feeding or reproducing can proceed, albeit at variable rates. These may be fairly broad, say ~12–28°C and ~50–90% relative humidity (RH) for cool, temperate insects. For *development*, the range is ~20°C, the *thermal window* (Dixon *et al.*, 2009), which gives an overall range of 13–30°C, with cool temperate insects often having wider *ranges* than tropical ones. But for six tropical trichogrammatid wasps, the *intrinsic rate of increase* (r_m) rises from a lower threshold of only ~10° to an optimum at ~30° falling rapidly to near zero at ~35° (see Fig. 2 in Kalyebi *et al.*, 2006). There is a zone below the favourable temperature range in which the insect becomes inactive, while above it there is a zone of hyperactivity (Section **10.1.1**). Finally, there are the upper and lower lethal zones (Mellanby, 1939; Fig. 10.3). For humidity, these zones are less clear cut and by comparison poorly studied (Tauber *et al.*, 1998). In all seasonal climates, however, *shortness of time* during which the environment is favourable is critical.

Different physical factors, noted above, often combine in their action on innate attributes. Thus, low humidity is often linked to high temperature, which, acting with wind speed, increases the drying power of the air. This would lead to desiccation and reduced survival, were insects not to take counter measures, both behavioural and physiological. Biotic factors often interact as well, usually the result of the complex, sequential nature of the food chain. Two enemy species may attack and possibly compete for the focal species as a victim. Then birds may consume these enemies and their victims that may be harbouring endoparasitoids that also perish.

Then there are influences in both directions between biotic and physical factors. Extensive plant communities are more *inter*active with their physical environment than are little insects, a result of scale (Levin, 1992). In beech woodlands the thick layer of autumnal leaf fall insulates tree roots, soil insects and other organisms from low winter temperatures and conserves moisture. The layer is

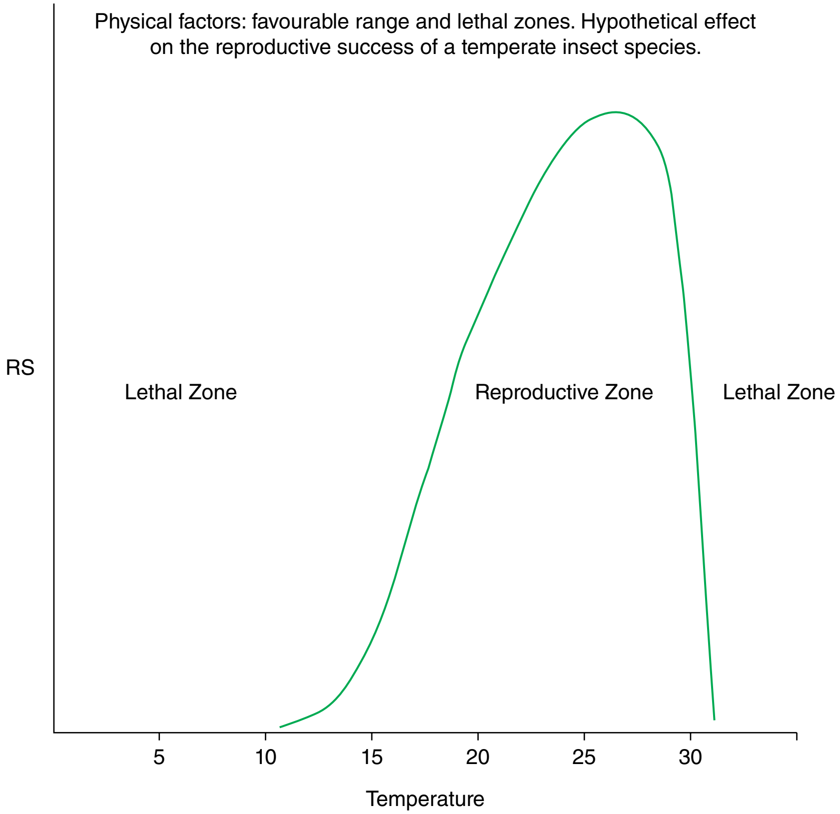


Fig. 10.3. Physical factors: favourable range and lethal zones. Autecological relationships often have this general form, with a sigmoid rise to an optimum and a rapid fall from it (see Figs 10.10 and 10.11).

thick because leaves occupy three-dimensional space on the tree, but essentially two-dimensional space on the ground. Then, after leaf fall the wind is less restrained by the trees. The pattern of tree growth and time of year affect the intensity, colour and pattern of light beneath the canopy (Endler, 1992). The term *ecosystem engineering* can be applied to such effects (Jones *et al.*, 1994, 1997; Danks, 2002; Ohgushi, 2008). Moisture supply influences the nitrogen metabolism of plants, which in turn affects their quality as food for herbivores (Mattson, 1980b). Then, physical elements of weather affect not only focal individuals, but also, either positively or negatively, those insects and other animals that directly influence them, especially their enemies. In cool weather, aphids and caterpillars continue to feed but their parasitoids cannot seek them (see above), as they do not fly. But birds still search for caterpillars, whose defences are concealment or distastefulness. Recall that external factors affect, again positively or negatively, although often in a rather diffuse way, the habitat and its resources. Such diversity constitutes the *ecological web* (Andrewartha and Birch, 1984). Real-world relationships often fall into more than one section of our classification, each overlapping related ones like conceptual roofing tiles. This is due to their *sequential nature* and to *diverse complexities*. Thus for a herbivore, temperature, nutrients and moisture affect food, which influences a female's size, then her maximum potential fecundity (MPF) and often her ability to distribute eggs. But if kept within reasonable limits, *cases of overlap and replication help us to wrestle with the complexity of nature.*

The physical elements of weather, influenced by topography, have *macro-effects* on habitats and *micro-effects* near individuals. Insects can modify their close surroundings (Turner, 2000; Danks, 2002) but not, excepting massive outbreaks, the physical environment of their habitat. Furthermore, widespread physical factors permit, or do not permit, individuals to pass through the matrix (Section **9.3**). Consider a *chain of events* caused by heavy rain in a *seasonal*, tropical forest on an exophytic caterpillar, say of *Hyblaea peura* (Section **5.2.1.4**(**k**)). This would have: (i) immediate micro-effects on these herbivores and their enemies by reducing their activity; and (ii) subsequent macro-effects on the habitat by promoting a general increase in plant growth. Later, *Hyblaea* would feed and spin cocoons, perhaps in folded leaves (Fig. 10.4), so modifying their microenvironment. In the longer term, habitat humidity would increase due to water held in the soil and to increased transpiration, which would then raise (engineer) the microenvironmental humidity near our focal individuals. In temperate forest in spring, rising temperature similarly drives the food supply (Danks, 2007). In extreme cases, rainstorms act as proximate mortality factors, killing individuals of our focal and other species and causing widespread habitat destruction by damaging plants and eroding soil. Keeping our classification tight, we see these events as factors affecting the innate attributes of our species. While increased rainfall soon produces better food for a herbivore, storms might cause an immediate shortage. But the food itself, its quality, scarcity or abundance, has direct effects on the herbivore's innate attributes and so RS. Here, rainfall is an *ultimate factor* and food is a *proximate* one (see above and Section **12.3.4.3**). Ultimate, intermediate and proximate factors usually exist.

Looking at these relationships in more depth, individuals and, by extension, the populations they comprise, have four innate, but diverse attributes. First, *development and growth*, the former defining the fact that developing eggs, pupae and adults do not get much bigger but change structurally by *physiological and embryological* processes. Second, *survival*, while basically *ecological*, is one in which the physiological mechanism of diapause and the largely behavioural ones of defence are often critical. Third, *movement*, which is not quite synonymous with locomotion, since the former term includes activities such as grooming, feeding and defence. Even so, while conditional on sensory input, movement is the basis of *behaviour* (above). Here *stage is key*. Eggs and pupae are immobile, although the latter may wriggle in defence. Nymphs, and with few exceptions (Sections **5.2.1.4**(**c**), **5.2.1.4**(**f**) and **5.2.1.4**(**g**)) larvae, move only within a limited ambit. Hence, winged adults are usually the most important instar effecting redistribution and the diverse behaviours employed in reproduction (Sections **1.3** and **10.2.4.1**). Finally, *reproduction* is even more complex, having physiological, behavioural and population genetic aspects. It includes not only natality *per se*, but also individual quality, the efforts of both sexes to donate their genes to posterity and progeny distribution and defence by females. This sequence is rather like that in an insect's life and the way they *combine to influence its RS*. Of course, life cycles have no end: egg quality influences juvenile quality, then adult quality, then egg quality. Diapause and death occur in any stage. Influences acting early, like growth, are easier to unravel than those acting late, especially reproduction.

Fig. 10.4. *Hyblaea puera* larva on a teak leaf. The moth can be an important tropical defoliator of this valuable hard wood. Source: Wikimedia Commons, author Balakrishnan Valappil.

There are three further points. First, just as diverse interactions co-exist between external factors, both physical and biotic, so sequential effects exist *between the attributes themselves*: growth affects survival, then achieved fecundity (AF), egg distribution and, ultimately, RS (Fig. 10.5), the sequence being influenced by genetics and environment. In Africa, the stem-boring larvae of *Busseola fusca* and *Chilo partellus* (Section **4.4.1.1**(**c**)) enter diapause, so surviving the dry season. But the longer they diapause, the lighter they become and the lower the AF of emerged females (Kfir *et al*., 2002). Second, we saw in Section **9.1** that innate attributes could be considered in relation to life-history strategies (Cole, 1954; Stearns, 1980, 1992), a concept of evolutionary ecology. Third, environmental factors are sometimes called 'environmental parameters'. 'Parameter' has a nice scientific ring to it, but also a clear meaning in statistics, being a property

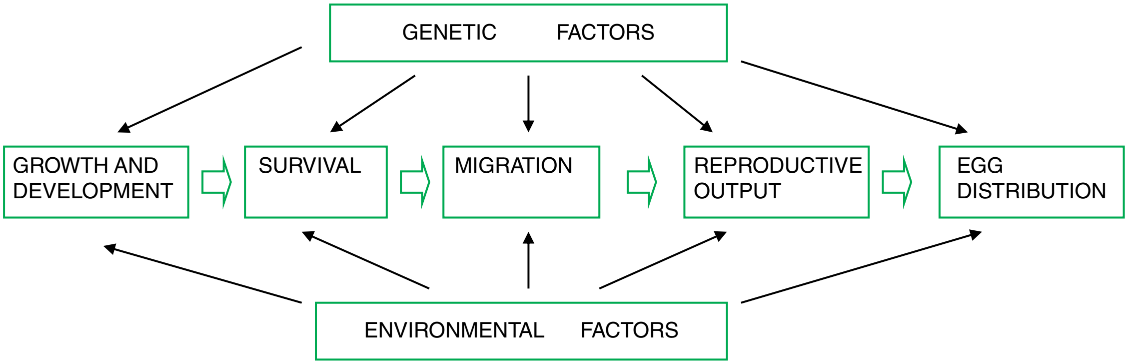


Fig. 10.5. Interactions between genetic and environmental factors in the life of insects.

of a sampling *universe* that is *estimated by a statistic* from homogeneous, empirical data (Bailey, 1994). Thus 'weather' is not a parameter, being inhomogeneous. The term should not be used loosely, 'factor' is perfectly good. We now consider *physical and biotic factors* in detail (Sections **10.1.1** and **10.1.2**), examining each *innate attribute* in relation to them in Section **10.2**.

10.1.1 Environmental factors: Physical

Here we consider global, topographical, edaphic, physical and chemical factors and also an abstract aspect: namely predictability. They are largely physico-chemical and/or properties of the non-living world (see Fig. 10.1). But on occasion they have a biological origin, such as the heat generated in a nest of bees, the sound of approaching wasps, more often volatiles from plants and CO_2 from organisms. We saw that these factors impinge on insects on decreasing scales. Globally they are the *invariant presence* and *predictable effects* of latitude, and locally of topography and soil (see below). Closer to the focal individual, however, there are seven *variable, physico-chemical* factors.

1. Heat from incoming solar radiation (*insolation*; Section **2.2.2.1**) and temperature. Temperature is the thermometric description of the energy content of matter, be it gaseous, liquid or solid. Like light (point 3), heat may radiate from objects. It is also picked up from them by conduction.

2. Precipitation (rain, dew, hail, snow), moisture of the air and/or of the medium in which the organism lives and the distribution of water available to it in its patch or habitat.

3. Light: the insect's visible part of *insolation*, its intensity (illuminance), direction and periodicity; and *reflected light* in the habitat, especially of *signals* coming from organisms: their colour (wavelength), contrast, object size, shape and pattern.

4. Mechanical factors are often the end result of heating and pressure changes in the atmosphere: wind, rainstorms, hail, but also water currents, sandstorms, landslides, earthquakes and volcanic eruptions (Section **12.3.3.2**). These factors deliver materials and affect points 1 to 3. They occur on very different spatial scales that often relate to their severity. Eruptions can alter the global climate. In the main, though, such physical factors are derived from weather in the short term and climate in the long term. Weather is *time dependent, climate time independent*.

5. Chemicals, linked to physical factors, are in the soil, on surfaces, and especially when air borne may constitute signals. They have more direct effects in the soil (edaphic factors) and in water. Calcareous materials in soil determine its acidity and fertility and so the nature of organisms there, e.g. *Tipula* spp. larvae (Freeman, 1967b; see below). The quantity of inorganic nitrogen in the soil strongly affects the type of plant community that develops. Plants on poor (*oligotrophic*) soils are deficient in this element (Mattson, 1980b), but plant associations on them can be complex (Huston, 1993). Pollutants from industry and agro-chemicals usually have negative effects, those of fertilizers being complex. Anthropogenic sources of nitrogen now exceed those from natural sources, altering plant distribution, biochemistry and breakdown by microbes (Jefferies and Maron, 1997). Apart from elements cycled by organisms (Section **10.1**), they produce many chemical compounds: volatiles from plants (Section **2.4.2**), pheromones and defensive compounds from insects.

6. Insects perceive sound and vibration. Organs in some crickets, cicadas, moths and beetles produce sounds. Some tephritid flies employ vibration in their courtship behaviour (Marsteller *et al*., 2009). Fleas in cocoons respond to it as an exit cue; parasitoids may so detect endophytic hosts (Bushing, 1965; Tomov *et al*., 2003; Vet and Dicke, 2011). Potential victims may detect the approach of wasps and tachinid flies by sound (Gross, 1993).

7. Finally, ionization may affect insects in flight (Maw, 1965).

Having defined these physico-chemical factors broadly, we now discuss complexities. Weather is modified by the invariant presence of topography (Burt and Pedgley, 1997), but it has two components of a different nature: one *predictable* and the other *unpredictable*. The former, due to the mutual mechanics of the Earth and Sun, results in the annual variation in day length during which insolation reaches Earth at a given latitude (Section **2.2.2**). The latter component (Southwood, 1977; Sandvik *et al*., 2002) is due mainly to the unique global weather patterns that arise from complex drivers (Rind, 1999). These exist as relatively short-term phenomena, being overlaid and influenced by the predictable component, and relate to *regional macroclimates*. Thus, in temperate areas there is a regular march of increasing photoperiod during spring, bringing increased radiant energy, elevated temperatures, and in train increasing plant growth. But superimposed upon this there is great variation due to the vagaries of weather (Rind, 1999; Danks, 2007). We may say spring is ‘unseasonably’ cold, warm, wet or dry. In the tropics, the predicable variation in solar radiation between days and seasons is less, so the unpredictable component of weather is more significant. In the seasonal tropics and deserts (Section **2.2.2.1**), there is great annual variation in the duration and intensity of the rains, whose patterns are, therefore, only partly predictable. But there is a well-established *inverse* relationship between mean annual precipitation (MAP) and its seasonal variation (Section **5.2.1.1(e)**). Regionally, there is autocorrelation of mean temperature and MAP, effects that die away with distance (Koenig, 2002), more rapidly so with MAP. Large-scale cyclic events such as the El Niño/La Niña cycle (Cane, 1986) and the North Atlantic Oscillation (Section **2.2.2.1**) also influence and may ultimately drive the weather and, in turn, insect populations in complex ways. It follows that predictability is a major concern in assessing future action in agriculture, including pest control.

The basics of the regional physical environment or of a plant community can be recorded as an annual *hygrothermograph* (Fig. 10.6). Cook, as early as 1924, used such plots when investigating the distribution of the cutworm *Porosagrotis* (Sections **3.2.1.2(e)** and **12.3.4.3**), while Thompson and Parker (1928a) used them to study regional differences in the ecology of *Ostrinia nubilalis* (Section **4.4.1.1(d)**). Today they are useful for climate matching to assess the suitability of potential biocontrol agents (Section **13.2.4.6**). An informative short-term graph records the diurnal changes in temperature and humidity (Fig. 10.7). Another simple physical index of an area is the precipitation/evaporation (P/E) ratio. Of course, evaporation is influenced by temperature, humidity and wind speed. For example, if 1000 mm of rain fell and 500 mm evaporated from a given area this ratio would be 2.0, the excess having run off to feed rivers or soak into the aquifer. If 500 mm fell and 1000 mm evaporated, the ratio would be 0.5 and water would have been drawn up from the soil. This ratio influences the distribution of plants and describes stresses to them if soil water is short. A more sophisticated measure is the *actual evapotranspiration* (AET), calculated from climatic data. The AET estimates total insolation, correct for the amount of this energy unavailable to plants due to aridity by accounting for mean monthly precipitation, estimates of evaporation, transpiration and the stores of soil water. It is a good *global predictor* of plant diversity (Wright, 1983) and hence, potentially, that of the insects depending on them.

To recap: the local aspects of temperature and water are the main physical drivers in insect ecology (Willmer, 1982; van Lenteren *et al*., 2006), while light and mechanical factors can have tangible effects. Individuals seek favourable hygrothermal sites and endeavour to maintain hygrothermal balance. Regional temperatures are driven primarily by the mechanics of the Earth and Sun, but are influenced locally by topography, winds and the nearness of water masses (Section **2.2.2**). In general, physical factors are altered by topography and *biologically engineered* by dominant organisms such as forests or herds of ungulates (Section **10.1.2**; Jones *et al*., 1994, 1997), both in direct relation to

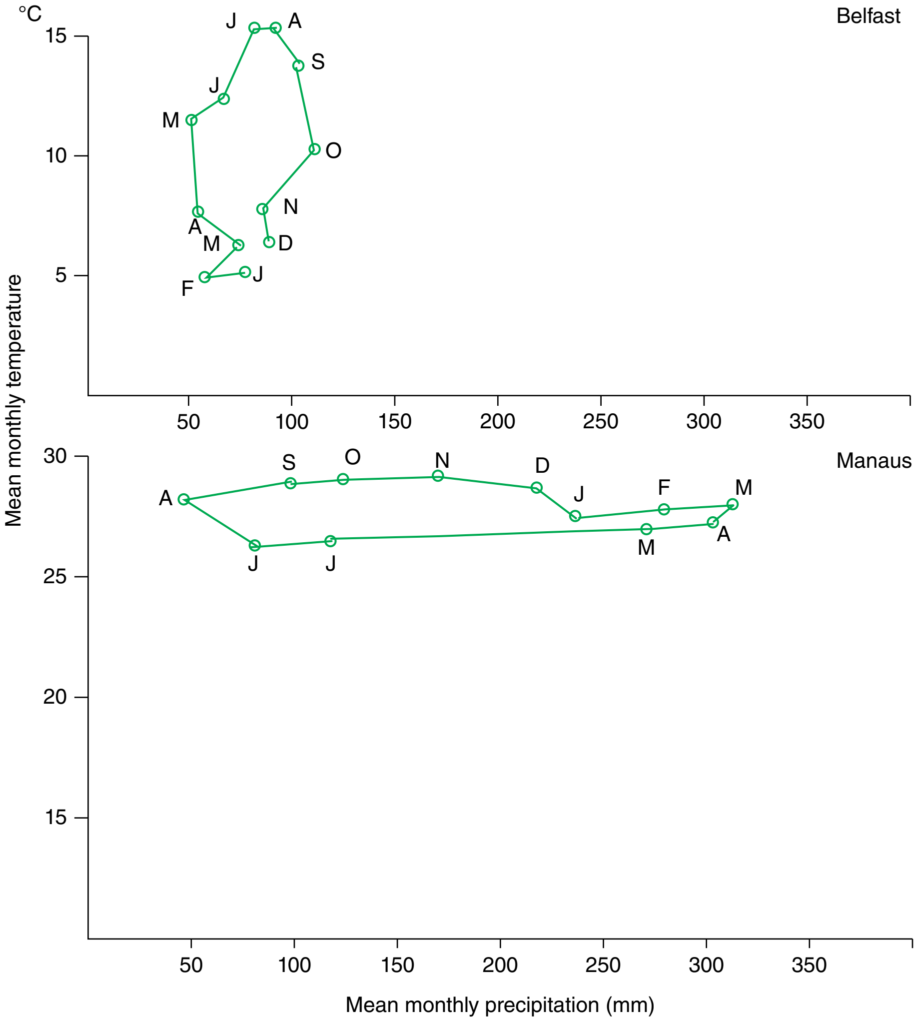


Fig. 10.6. Mean monthly rainfall versus mean monthly temperature. The hygrothermograph expresses the great difference between temperate (Belfast) and tropical (Manaus) climates. Even so, the variation in humidity would be less in the forest adjacent to Manaus.

their mass. Our own species is of course a major engineer. Regionally, forests modify the albedo (Section **2.2.2.1**), locally woodlands reduce hygrothermal fluctuation (Freeman, 1965; Holling, 1992; Leather *et al*., 1993). Moisture has two sequential phases: (i) precipitation; and (ii) the subsequent fate of the water (Section **10.1**), whether gaseous or liquid. Below zero, water becomes ice or snow, affecting the microenvironment, but is unavailable to insects until it melts. Precipitation is measured easily; atmospheric humidity is more complex. How far short of saturation the air may be is *relative humidity* or *saturation deficit* (q.v.). Then the *drying power of the air* involves temperature, saturation deficit and air speed. This factor is often key for insects because their small size and hence relatively great surface area (Section **1.2**) make them potentially vulnerable. Below we sample some complexities, which relate essentially to spatial scale (Levin, 1992).

So weather has macro- and micro-effects, the latter being the lower end of the spatial scale of physical drivers. The weather insects experience would not be recorded on Stephensons screens used in

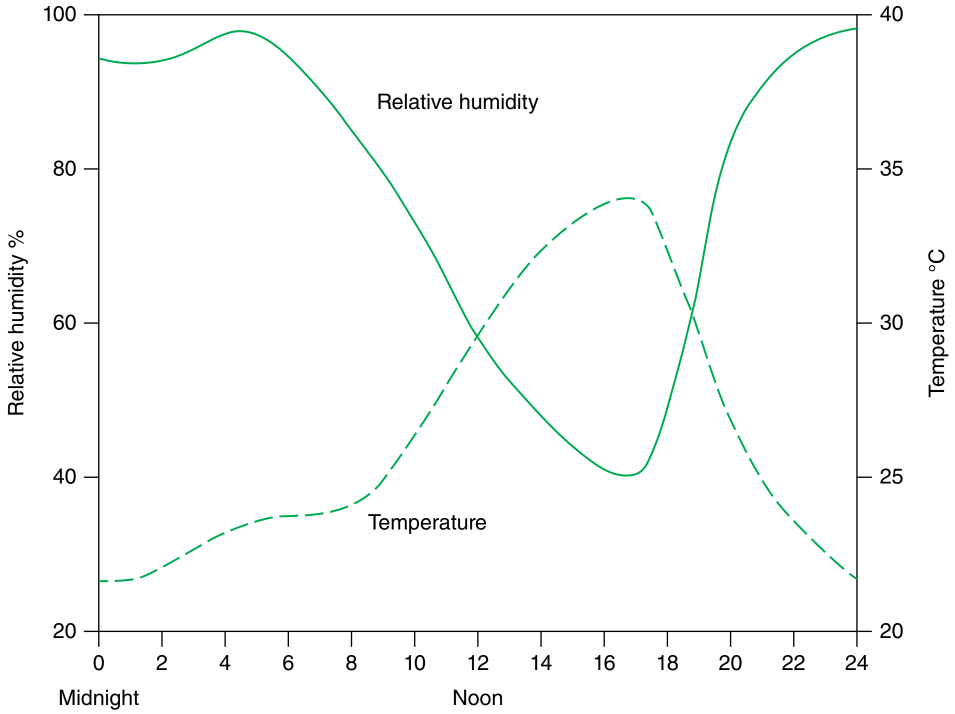


Fig. 10.7. Diurnal variation in temperature and humidity. The figure is typical of summer conditions in a mid-temperate region.

meteorology, which are standard in form on standard grassy patches, both to reduce local influences. The weather affecting insects is modified by their surroundings, firstly at the habitat and patch levels, and finally in their immediate vicinity (Section **9.3**). Modifications that occur may be influenced by either *inorganic*, largely topographical features on descending spatial scales (hills, lakes, streams, rocks, hollows and banks) or *organic* features such as plants. These effects result in what is often called *microclimate*. But the rapid changes that occur from hour to hour that influence insects should really be called '*microweather*' (den Boer, 1968; den Boer and Sanders, 1970).

An example of physical modification on a macro-scale occurs in a gorge. The rock walls provide shade, areas of dryness and alter wind patterns. Solitary wasps build their nests beneath overhangs (Freeman, 1977, 1981a; Taffe, 1983). Ant lions are found there only in soils sheltered from rain. The wadis of the Sahara provide areas in which recession populations of desert locusts (Section **5.2.1.1**) persist (Ibrahim, 2001), as their topography concentrates available moisture. On a micro-scale, ants nesting under stones use a modified physical environment. *Aedes punctor* lays eggs in a narrow horizontal band within forest depressions (Fallis and Snow, 1983). In autumn, these fill with rainwater and the eggs hatch. While big stones protect the soil beneath from rain, they rest in depressions into which water runs, and reduce evaporation. Microtopography influences wind and water distribution on the scale of a metre or two, the former being material for weakly-flying insects less so for those with high ISC (see Section **10.2.4.1**).

Biotic modifications are even more diverse. Thus, insects living in the foliage of a forest tree are sheltered by the forest itself and then by the tree's canopy. They are shielded from insolation in an envelope of low light intensity and enhanced humidity (Lee, 1978) and protected from mechanical damage from rain and hail. The tree is an *ecological engineer at the patch level*. If they lived in an isolated tree instead of one in a forest, protection would be less. *Habitats engineer the physical environment of patches* (Sections **10.1.2** and **12.2**).

Large patches may *engineer physical heterogeneity* within themselves. If a moth pupates under the tree it fed on, the canopy stabilizes the physical properties of the soil beneath, shielding it from excessive insolation, from showers and draws water from it by transpiration, while the roots reduce erosion. On cold, damp nights, mist condenses on this canopy and water drips onto the ground below.

Such within-patch heterogeneity is pervasive and roughly depends on patch size. In beech woods insects often live on lower branches, physically the most protected regions (Nielsen and Ejlersen, 1977; Phillipson and Thompson, 1983). In the UK, the bagworm moth *Luffia* prefers lower levels of trees (McDonogh, 1939). In Canada, *Lithocolletis salicifoliella*, a gracillariid miner, prefers the lower foliage of poplar (Martin, 1956). In Jamaica, *Papilio homerus* larvae inhabit only the lower parts of *Hernandia* trees (Garraway *et al*., 2008). In New Jersey, *Papilio glaucus* lays 97% of the eggs at 0.5–2.5 m on trees, but prefers sunny exposure and develops faster there (Grossmueller and Lederhouse, 1985). In Europe, the leaf miner *Cameraria ohridella* is denser in the lower levels of horse chestnut trees (**Fig. 10.8**). Similarly, in Arizona, higher densities of two leaf-mining moths occurred in shaded rather than in exposed oak foliage. But in two associated species, this effect was weak (Bultman and Faeth, 1988; Section **10.2.5.5**). Here, leaf quality and rates of parasitism were also related to shade. In an extensive survey in Missouri, herbivorous insects in the oak canopy were different from those underneath it, although this had multiple causes (Forkner *et al*., 2004). In Japan, *Pieris rapae* prefer to oviposit on the under surface of cabbage leaves (Tagawa *et al*., 2008). Again in Canada, *Pemphigus betae* (Section **3.3.3.1(a)**) lay most of the eggs in the lower levels of poplars (Harper, 1963). The tachinid fly *Compsilura concinnata* is a more effective parasitoid of gypsy moths low down in trees (Weseloh, 1982). While there is much evidence for greater insect activity at such levels (Hespenheide, 1991), in contrast, *Hypsipyla grandella* (Section **4.2.1.2(n)**) prefers exposure. *Malacosoma californicum* seek the sunny side of big red alder trees for oviposition (Moore *et al*., 1988), while *Conophthorus* beetles (Section **6.3.1.1(c)**) avoid cones in the lower levels of pines, although often suffering from lethal high temperatures above (Mattson, 1980a).

Fig. 10.8. Distribution of *Cameraria ohridella* larvae on a horse chestnut tree. Damage tends to be greater lower on the tree.

To continue: north temperate beetles under bark on the south side of an *exposed* tree trunk can be ~8°C warmer during a summer afternoon than those living on the north side. There are also differences in temperature regimes due to properties of the bark (Nicolai, 1986), differences that would be far less within the shaded interior of a forest or during cloudy periods. But as we noted, insects often move between parts of their patch to find better hygrothermal conditions. *Primary species* build nests, cocoons, burrows and other shelters (Berenbaum, 1999; Danks, 2002, 2007), improving microweather (Willmer, 1982; Duman, 2001) and saving energy (Turner, 2000). Such structures are used by *secondary species*, as in the case of secondary solitary wasps (Freeman, 1974). Caterpillars in the Gelechioidea tie up leaves with silk, improving their own environment but also that for some other contemporary and subsequent species (Lill and Marquis, 2003). Tortrix larvae roll leaves, while those of lackey moths (see Fig. 5.5 and Section **5.2.1.4**(**e**)) spin communal webs around the twigs of their food plant, serving as a protective retreat. No amount of spinning would be effective without this framework. Thus, while insects obviously cannot determine the weather, they can modify its impact and may engineer it on fine spatial scales. Clearly, any physical measurements ecologists make must be exactly where individual insects live. Unwin (1980) and Nicolai (1986) give technical details for this.

Physical factors affect innate attributes as follows. For temperature, the *favourable ranges* (Section **10.1**) are generally widest for survival, less for growth and least for reproduction. Warmth is needed for more energetic locomotion and hence for flight rather than for walking. At *lethal high temperatures* mortality increases progressively with temperature and time. At *lethal low temperatures* individuals adapt variably to survive extremes. While temperature affects the growth rate directly, the duration of favourable temperature permits, or does not permit, juvenile development in a given season (Section **10.2.2.2**). Atmospheric humidity also reduces growth and survival if it can enter and disrupt an individual's physiology. But rainfall, or better, precipitation, humidity and water distribution are all related (see for *Hyblaea*, Section **10.1**). If there is no rain, humidity falls gradually and water sources dry up at a rate directly related to temperature and their degree of exposure but inversely related to humidity and their size. We saw (Section **2.2.2**) that rainfall is a major determinant of the nature and diversity of plant communities and hence the animal communities that depend on them.

Light intensity, wavelength and duration are critical factors for plants since, if other factors are not limiting, they determine photosynthetic rate and hence plant growth. But insolation includes heat as well as light: well-illuminated places are warmer and become drier than shaded ones. Incident light drives vertical stratification (heterogeneity) in forests. Growing trees shade out lower levels, reducing and ultimately prohibiting plant growth and diversity beneath (Smith, 1973). Such *overstory competition* reaches ultimate limits in beech woodlands, coniferous forests and selva, leading to a depauperate insect fauna near the ground, although in selva a few plants such as *Dieffenbachia* (Araceae) and some ferns can grow in the dim light. Indeed, <2% of the light useful for photosynthesis that hits the canopy reaches these areas (Chazdon and Fetcher, 1984). Many Araceae are pollinated by Diptera, which are lured to flowers that mimic several properties of carrion: breakdown products, CO_2 and even heat. They employ chemical mimicry (Dettner and Liepert, 1994). This contrasts with most plants, which employ a high intensity of reflected light from their flowers (Section **8.2.1**).

Many insect species use diurnal periodicity and the progressive annual change in day length as cues to track the predictable part of weather. Unlike temperature and moisture, the photoperiodic aspect of *incident* light is unmodified by the microenvironment, although its intensity may be reduced and its spectral quality modified. While light does not normally disrupt insect physiology, *Plutella xylostella* (Section **5.2.1.4**(**a**)) are more fecund in long-day conditions (Harcourt, 1957), possibly because females can be active for longer.

Apart from *incident light*, insects respond to *reflected light* from objects in their habitat (Prokopy and Owens, 1983). Usually their vision is trichromatic, with special sensitivity to UV (~350 nm), blue (~440 nm) and green (~550 nm) (Section **8.2.1.1**; Briscoe and Chittka, 2001, who give an extensive table of spectral sensitivities). But the dragonfly *Sympetrum rubicundulum* has sensitivity in five peaks, one into near-red (620 nm). *Papilio xuthus*, several other butterflies and the sawflies *Tenthredo* also see near-red (600 nm). Scarabaeid beetles, but almost no bees, can see red, while most *Bombus* see violet-blue well. *Spodoptera exempta* is sensitive to infrared (Langer, in Hinton, 1973), and *Melanophila acuminata* (Buprestidae), using special thoracic receptors, also responds to it (>750 nm). These odd beetles arrive at the aftermath of forest fires, preying on moribund insects and ovipositing on the burnt stumps (Evans and Kuster, 1980). In several insects, green receptors are confined to the ventral parts of their compound eyes, presumably the better to monitor foliage. For herbivores, young foliage with high levels of nitrogen confers a yellower appearance than mature foliage (Prokopy and Owens, 1983) and hence attracts them. There is physiological evidence that a red receptor, common in butterflies, is necessary to distinguish different shades of green (Kelber, 1999). The presence of a near-red receptor in phytophagous sawflies, but not in other Hymenoptera, gives further credence for this conclusion. But as noted, the quality of *ambient* light affects that emitted by objects (Endler, 1992). The spectral quality and pattern of light reaching insects in nature at an instant and available for an appropriate response is extremely variable.

Some soil insects prefer either acidic (e.g. the beetle *Popillia*) or alkaline (e.g. the wireworm *Limonius*) conditions. In aquatic environments the acidity of the water (pH) is an influential physical factor, as in larvae of the Tipulidae (Freeman, 1967b), Culicidae, Chironomidae and Simuliidae. Oxygen tension is often critical, especially if the insect breathes with gills instead of from the surface air. Water can contain less dissolved oxygen at higher temperatures, although an insect's metabolism, and hence oxygen requirements, are greater. The diurnal fluctuation of temperature is damped according to the mass of the water body, and the mechanical effects of current speed are further factors. In another physical interaction, fast-flowing, high-gradient streams bring cool, well-oxygenated water from higher altitudes, another topographical influence.

10.1.2 Environmental factors: Biotic

Unlike the spatially graded action of physical factors in habitats, patches and close to individuals, biotic factors, whether plant or animal, usually operate at or near the point of contact of a focal individual and another organism. For example, two *Papilio* males jostle for a territory; a parasitoid female oviposits in its victim; or a plant deters a herbivore with chemicals in its cells. While extensive biotopes have widespread, engineering effects, they typically *modify physical factors*, not cause them. Biotic ones often form *food chains*. As discussed in Section **10.1**, the density of a focal species is a *unique biotic factor* operating all the time, which gives rise to several *intraspecific* effects. These are usually negative (dis-operation, competition, cannibalism), less commonly positive (co-operation). As the negative effects are generally held to have the greater impact on insect populations we deal with them first, together with some intricacies.

Intraspecific competition for a limited resource results in a trend of increasing harm to individuals, from trivial, to reduced RS, to death (Section **9.8**). But when conspecific individuals kill and eat each other it is *cannibalism* (Fox, 1975; Polis, 1981) *not competition per se*: they do not seek the same resource, unless it is space. If so, situations that are initially competitive may result in the death of one individual, perhaps in cannibalism. Such *intraspecific predation* is often found in diverse *carnivorous* insects: dragonfly nymphs, the aquatic bug *Notonecta*, the larvae of the mosquito *Toxorhynchites,* triatomine bugs, lacewings and ladybirds. But it is also found in larval *Tribolium* and *Leptinotarsa* beetles, *Cydia, Heliothis* and *Callimorpha* moths, aphids and pyrrhocorid bugs (Banks *et al*., 1968; Richardson *et al*., 2010) that are otherwise *herbivorous*.

Here are some more subtleties. If two codling moth larvae meet in an apple and one kills and eats the other, it is not competition for food or space, for they are abundant, it is just *cannibalism*, with the victor's advantage being *enhanced nutrition*. Resource competition might well reduce the RS of both individuals, but cannibalism results in zero RS for one and higher RS for the other. When two *Anthocharis* (Section **9.1** and **9.8**) larvae contest the *limited* territory of a flower head, and the loser is ejected, it is competition for space. But if the loser gets eaten, such competition results in cannibalism (Baker, 1983). *Anthocharis* females may compete for flower heads using an oviposition deterring pheromone (ODP; Section **8.2.2.4**(e); Dempster, 1992), a behaviour reducing subsequent attrition. But they do not fly in cool weather (Section **10.2.5.3**), so they cannot compete. In my experience, however, huge amounts of its food plant(s) exist without any larvae, so that harmful effects must be local, slight or absent. Suppose realistically that in a population of 1000 *Anthocharis* two larvae are killed like this, competition would be trivial for the population.

An odd situation occurs in parasitic wasps, such as *Aphytis* (Section **8.2.2.5**(**o**)), since females may kill hosts already parasitized by a conspecific female. In *Encarsia* and *Coccophagus*, which are endoparasitoids of scale insects, the rare male larvae hyperparasitize conspecific female larvae (Askew, 1971). In ladybirds, cannibalism of *Adalia bipunctata* eggs by young larvae occurs on non-sibling egg batches (Mills, 1982), and in *Harmonia axyridis* there is even cannibalism between siblings (Kawai, 1978). Here, ~25% of the eggs were eaten but survival of the cannibals enhanced. One might think that laying larger eggs with more food could also increase larval survival, but cannibalism ostensibly selects for faster egg development. If two *Cephus cinctus* larvae (Section **4.4.1.1.**(**b**)) are in the same stem, a parasitized one is more likely to be cannibalized than vice versa.

In all, cannibalism is widespread and ultimately may form a significant element of population regulation. Its occurrence may result from genetical differences and from environmental drivers such as scarcity of normal prey; especially from high conspecific density relative to resources. There are no time lags (Polis, 1981; Section **11.5.1**) and regarding energy flow it forms a loop retaining energy in a population. In so doing, however, it may facilitate the vertical transmission of pathogens (Section **7.3.2.4**(**b**)). When individuals in societies kill but do not eat each other it is *warfare*, as occurs between adjacent nests of *Camponotus hannani* ants in Jamaica. Such territorial wars are the end point of competition for space. But some ant species use other ants as their slaves, a more productive employment of victims, an example followed by man in many societies.

Other biotic factors comprise either living or dead organisms or their products of other species (Section **9.8**). But living, *heterospecific species have the potential for more far-reaching interactions with focal individuals* than dead ones do. In synecology, they are part of the food chain and so are involved in interwoven trophic pathways. They are potentially *endogenous factors,* showing flexible behaviour in the present and evolutionary change through time (Janzen, 1980; Connell, 1980; Vermeij, 1994). Dead organisms play a passive role, often providing shelter and food, for example a fallen, rotting tree or an avian carcass.

To recap, the action of physico-chemical factors on individual attributes of a focal species and its associates, *is generally one way*. Thus, the action of temperature on growth is entirely of this type even though many insects can modify their surroundings advantageously (Turner, 2000; Section **10.1.1**). Ambient temperature affects the growth rate of some caterpillars, but they do not alter today's temperature within the habitat. With living biotic factors, however, there is *often a two-way interaction*. Thus, the consumption rate of living food may alter its rate of supply (Andrewartha and Birch, 1954). This is typical of interspecific interactions (Elton and Miller, 1954), often those in the food chain. Visualize the tops of broad bean plants stunted by a mass attack of *Aphis fabae* to realize this truth. Dead food like detritus and carrion does not react like this. Herbivorous insects, excepting those attacking seeds, rarely kill the plant they attack and may have subsequent effects on other insects following them (Ohgushi, 2008). I will point out below several such interactions.

Living, heterospecific organisms may engage in a spectrum of negative or positive interactions with focal individuals. Although these are two-way, the results are often negative for our species, as Lord Tennyson put it: 'Nature, red in tooth and claw'; a vertebrate bias! Enemies may inhabit the same place as the focal species or be visitors, a meaningful distinction in reality, as models (Section **11.5.3**) usually assume the former. *Victim* is a good, inclusive term for the prey or host. While enemies often kill members of a focal species, obtaining food for themselves and/or their progeny, and reducing the survival of the victim's population, they may also have less dramatic effects (Lima, 1998; Preisser *et al*., 2005; Nelson and Rosenheim, 2006). Thus, a potential victim that drops from a plant to avoid an enemy has to find its way back, wasting time and energy, risking death through getting lost, dying in a hostile physical environment or being eaten by a different predator. All or any of the defence mechanisms that potential victims possess (physical, chemical, physiological, deceptive, cryptic) may be employed in defence. Some victims avoid attack, others thwart attack. Of the latter, some means are *constitutive*, others are *induced*. The tough exoskeleton of many beetles is constitutive; the immune reactions of hosts against endoparasitoids are induced. While potentially lethal enemies often fail to kill, there may be subsequent negative effects on the growth, survival, reproduction and movement (Nelson *et al*., 2004) of their victims. Sometimes the avoidance reactions of potential prey towards one predator, make them difficult to capture by another one, another facet of competition (Preisser *et al.*, 2005). In all, enemies kill or disperse their victims, but parasitoids, unlike predators, are very often killed by their hosts (Section **10.2.3.8**).

Other living species also influence our focal species in diverse ways. Certainly, the most important of these are plants that provide herbivorous insects, including our crop pests, with food. But if the focal insect is a carnivore we must consider its animal, usually its insect, food. There are also the tetrapod victims of ectoparasitic and micropredatory insects (Section **7.1.1**). Many organisms, both as individuals and populations, naturally function to localize or concentrate resources, namely organic localization (Section **9.8**). Growing trees cause a progressive increase of localized food and shelter for caterpillars. When a tree dies it is home to sequential waves of fungivores, detritivores and their enemies (Hamilton, 1996). Large mammalian herbivores drop great masses of dung, giving food and shelter for sequential communities of flies and beetles. Ultimately, mammalian carcasses provide rich pickings for other communities of detritivores (cf. Section **8.3.1**).

Andrewartha and Birch (1954) proposed a category of animals that were not enemies, food, or competitors, but even so caused *either deterioration or amelioration* in the immediate environment of a focal species. In their 1984 book, they placed such organisms in the peripheral environmental 'web' of a species. *Interaction webs* is a recent term to include such relationships, also touched on by Mayr (1963, p. 69). Cole (1949), using contingency tables, considered the measurement of interspecific association long ago. The area has been much researched recently (Wootton, 1994; Moran *et al.*, 1996; Polis and Strong, 1996; Gange and Brown, 1997; Bezemer *et al.*, 2003; Lill and Marquis, 2003; Ohgushi, 2005, 2008; Marquis and Lill, 2007). There are not just *cascades* of energy and nutrients flowing down between each trophic level, but reticulated links of various strengths forming the web (Smith, 1957; Darnell, 1961; Levine, 1980; Polis and Strong, 1996; Wootton and Emmerson, 2005). While these links are often used to investigate community structure, we are concerned here with their autecological effects, as were Andrewartha and Birch, and indeed Smith.

Some such organisms, while not being resources, are called *ecosystem engineers* (Jones *et al.*, 1994, 1997; Sections **10.1** and **10.1.2**), modulating resource supply to other species and having *positive or negative influences* on their RS. They are *non-predators, do not share resources* with our focal species, yet influence its chance to survive and multiply (Nicholson, 1933, p. 141; Andrewartha and Birch, 1954, p. 400). Mattson and Addy (1975) use the term 'regulators' in a related context. But supplying a resource and modulating its supply are not mutually exclusive. Trees may supply food, but also modify the microenvironment of caterpillars by altering both physical and biotic factors (Section **10.1.1**; Polis and Strong, 1996). Organisms creating new environments, like trees forming woodland biotopes and clonal plants forming patches, are *autogenic engineers*. Those modifying existing habitats or patches are *allogenic engineers*. In southern England, hillsides grazed by sheep promote a suitable habitat for the butterfly *Hesperia comma* (Hill *et al.*, 1996). Lill and Marquis (2003) even regard forest caterpillars as engineers as they increase biodiversity. But when species modify their immediate surroundings for their own ends, as in social wasp nests and cocoons of moths, this is a phenotypic extension subject to natural selection (Dawkins, 1982; Turner, 2000). In *Sceliphron* (Section **8.2.2.4(n)**), large females make thicker mud cells than do small ones (Freeman, 1981c), their offspring having better survival. This engineers more resources for secondary wasps (Section **10.2.3.9**) that use the vacated cells. Apart from there being autogenic and allogenic engineering, such modifications occur on a range of spatial scales (Levin, 1992).

Many species form strands of diverse '*indirect interaction webs*' (Andrewartha and Birch, 1984; Marquis and Lill, 2007; Ohgushi, 2008). They can have positive or negative results for the focal species, often involving engineering; but if food is the link, *trophic interactions* occur. Here are some examples:

- Alternative victim species can maintain an enemy when the focal species is absent. *Swammerdamia* in the *Diadegma*/*Plutella* interaction (Section **5.2.1.4(a)**) is a *positive trophic example*.
- Trampling cattle compact pasture soil making it hard for grasshoppers to oviposit, which is *negative engineering and non-trophic*.
- But when cattle drinking at shallow ponds in African savannah leave water-filled hoof prints, they greatly improve the habitat for several mosquitoes, which is *positive* engineering.
- When scarabaeid beetles bury dung they increase soil fertility leading to better plant growth and

improved quality and quantity of food for various herbivores, a *positive trophic* effect.

- Competition between forest trees causes death of weaker ones, providing food for many beetles (Section **4.2.1.2**).
- *Mecas inornata* (Cerambycidae) girdles sunflowers, improving their food quality for *Melanoplus differentialis* (Lewis, 1984).
- *Malacosoma californicum* larvae eat red alder, improving its quality for *Hyphantria cunea* feeding later, increased RS resulting (Williams and Myers, 1984, in Ohgushi, 2005).
- When *Bathyplectes curculionis* attacks *Hypera postica* (Section **5.2.1.2(f)**) feeding on lucerne, it is attracted initially to the honeydew produced by *Acyrthosiphon pisum* also feeding there. The wasps do not affect the aphids but the level of parasitism on the weevil is increased (Evans and England, 1996).
- Various big ichneumons and tachinid flies, which do not affect little aphids, commonly feed on their waste honeydew. Note that *organic localization* (above) is usually involved with the operation of these effects.

Next there are co-evolved systems with mutual benefits, the so-called 'positive–positive interactions'. In a population and mainly among *related individuals* (Hamilton, 1964, 2001), we often see co-operation or parental care. In the former a tendency for some individuals to cheat remains, so that conditions favouring co-operative evolution are not simple (Axelrod and Hamilton, 1981). Siblings may co-operate as in communal web spinning by larval *Malacosoma* spp. (Joos *et al*., 1988; Section **5.2.1.4(e)**). Now if some larvae did not spin, so reserving internal resources, they might well grow larger and have greater RS, particularly as silk is metabolically expensive. But for *M. americanum,* this seems not to be so (Fitzgerald and Willer, 1983). For parental care, many females take time and risk to distribute the eggs on suitable food (below), so enhancing their own genetic fitness. Complex behaviour like this is found in solitary wasps (Section **8.2.2.4(n)**), who select breeding sites, build nests, lay eggs, provide food for the larvae and may spend time guarding them (Krombein, 1967; Freeman and Johnston, 1978a). Female tsetse nurture a larva within a uterus and place it when mature in a suitable pupation site (Section **7.3.2.4(m)**). In social Hymenoptera, related worker females co-operate in the nest to rear related offspring (Malyshev, 1968; Wilson, 1971). But in the beetle *Nicrophorus, a pair* of adults co-operates to inter a small tetrapod, an infrequent case of unrelated male and female insects assisting each other to increase the survival of their mutual offspring (Wilson *et al*., 1984; Scott, 1998). Males release a pheromone that attracts females, and when breeding perform diverse defensive behaviours. Sometimes more than a single pair co-operate (Hamilton, 1996). Such behaviour occurs in dung beetles: *Sulcophanaeus* (Klemperer, 1983b), *Onitis, Copris,* (Giller and Doube, 1989) and *Onthophagus* (Sowig, 1996; Emlen *et al*., 2005). In desert tenebrionid beetles, *Parastizopus armaticeps*, females prefer large males that dig deep burrows, thus reducing desiccation, while they collect dry vegetation as larval provisions (Heg and Rasa, 2004). More diffusely, the presence of males increases the searching efficiency of females in the encyrtid hyperparasite *Cheiloneurus paralia* (Kfir *et al*., 1976). Some male bark beetles, as in *Phloeosinus serratus* (Garraway and Freeman, 1981), attract several females to a boring that they have initiated, rejecting ones they deem unsuitable. Lastly, there is the case in which conspecific largely unrelated *Dendroctonus* beetles assist each other in the mass attack of a pine tree.

But there are many cases of *very different* species assisting each other (Wilson, 1997; Bronstein, 1998), an association called *mutualism*. If mutualists live intimately within their host, the term *symbiosis* is appropriate and commonly involves microbes (Smith and Douglas, 1987; Baumann, 2005; Moran, 2007). Symbionts spread since they increase the fitness of their hosts directly, and of course, of themselves. About 36% of the British insect fauna employ symbionts (Speight *et al*., 1999), a value that will certainly rise with future research. Examples are microbes in the guts of herbivores and detritivores, and in special organs inside beetles and sap-sucking bugs (Section **10.2.2.6**). But there are also very different mutualisms between sap-sucking homopteroids and ants, between ants and thorny shrubs, and between flowering plants and their pollinators (Section **8.2.1**). These lack genetic affinity and the benefits that accrue are *products, protection and transport*. Finally, there are many organisms living together that have little or no effect on each other. The lower the overall density of all the insects involved the more likely it is that this situation obtains, leading to a '*non-interactive community*' (Cornell and Lawton, 1992). So one expects a continuum of interactivity in insect assemblages, from considerable to little biological interaction. But again, physical factors have primacy.

Just as habitat and patch architectures (heterogeneities) modify physical factors (Section **10.1.1**), they also affect biotic factors. This is often due to what we can call their *microtopography* (see Levin, 1992). Coccinellid larvae and anthocorid bugs, among other predatory insects, search the *prominent contours* of plants for their aphid prey (Carter and Dixon, 1984). Tropical *Polistes* wasps, hunting for lepidopteran larvae in daylight, typically search the *surface of a plant* (patch), a danger zone in time and space for their prey (Section **9.9**). Indeed, caterpillars often seek the interior or base of a plant during the day and feed only at night when such predators are inactive. Larger larvae of the tropical moth *Melipotis* feed at night in the canopy of poinciana trees, but retire to its base in the day. The tree's architecture provides food (leaves), pathways for diurnal movement (branches) and refuges (under flakes of bark and fallen material under the tree). So part of a resource may be inaccessible to a searching predator (Andrewartha and Birch, 1954). *Aonidiella aurantii* (Section **6.3.2.2(a)**) in the interior of citrus trees are rarely parasitized by *Aphytis* (Murdoch *et al*., 1995, 1998), the patch having a zone of partial refuge. Similarly, larval *Ostrinia* (Section **4.4.1.1(d)**) in lower maize stems are beneath the search level of the parasitic wasp *Simpeisis viridula*. Then again, some plants are genetical mosaics (Whitham and Slobodchikoff, 1981; Orians and Jones, 2001), giving variable resource quality and *microtopography*. The shelters some insects build provide protection from predators as well as from harsh hygrothermal conditions (Danks, 2002). Sometimes resources are inaccessible at spatial scales greater than that of the habitat, thus tsetse rarely bite far from shaded areas. In all, the places in which insects live are heterogeneous, and Lynch *et al*. (1998), among others, have modelled the effect of refuges on the interactions between parasitoid and host.

10.2 A Survey of the Interactions

10.2.1 General introduction

There has been a long-standing trend to discount the physical environment and emphasize the biotic one, the likely result of the value given to mathematical models in which *physical factors are ignored* (Sections **10.1.1** and **11.5.1**; Tauber *et al*., 1998; Walter, 2003, p. 92), or seen as noise (Halley, 1996). As an example, the text on population ecology (Begon, *et al*., 1996b), has chapters on intraspecific competition, population models, interspecific competition and predation but no chapter on the physical environment. Wellington (1954) warned of this omission and Dempster and McLean (1998) stressed the 'enormous direct and indirect impacts' of physical factors on insect populations. Thus, the North American drought of 1987–1988 led to population crashes of many species (Hawkins and Holyoak, 1998). Cold tolerance is 'surprisingly understudied' (Lyytinen *et al*., 2009), and thermal extremes have often been neglected in work on range limits (Gaston, 2009a). Turchin (1999), a major figure in contemporary biomathematics, says that physical factors '… are not noise to be tuned out'. Fortunately, there are signs in current literature that physical factors are again being given due weight.

Insects are sensitive to hygrothermal variables (Willmer, 1982), vulnerable to adverse weather, their genetic variation often being attuned to mitigate such physical challenges. For polymorphism, there are seasonal changes in the frequency of chromosomal inversions (q.v.) in *Drosophila* relating to temperature (Dobzhansky, 1943). For *D. setosimentum* in Hawaii, climatic variation drives ~70% of the genetic variation (Bryant, 1974). It is greater at high altitude, where the physical environment is harsher and more variable (Steiner, 1977; Section **2.2.2.2**). In West African *Anopheles gambiae* the frequency of such inversions varies spatially and temporally according to hygrothermal variation (Coluzzi *et al*., 1979, in White *et al*., 2011). Even under warm Caribbean conditions, altitude and rainfall limit the distribution of several solitary wasps (Freeman and Taffe, 1974; Freeman, 1977, 1981a, 1982; Ittyeipe and Taffe, 1982; Section **12.3.4.4(h)**). There are many effects of weather on the population ecology of aphid parasitoids (Campbell *et al*., 1974; Weisser *et al*., 1997; see below). Hygrothermal variables explain the distributions of *Ceratitis capitata* and *Lymantria dispar* (Gevrey and Worner, 2006). But in comparative laboratory work on trichogrammatid wasps, temperature has more effect on life-history traits than humidity (Kalyebi *et al*., 2006). However, the effects of physical factors may be unseen in life tables (Section **11.4.1**), they may not kill directly but permit enemies to do so.

So, marginalization of the physical environment is a trend we shall not pursue. The outcome of biotic interactions usually depends on prevailing hygrothermal conditions (Thompson, 1929; den Boer, 1982; Turchin, 2003; Parmesan, 2006; Danks, 2007). Field predation on young larval *Delia radicum* (Section **3.2.2.1(i)**) by carabid beetles is largely temperature dependent (Hughes and Mitchell, 1960), as is the ability of *Encarsia formosa* to parasitize populations of *Trialeurodes vaporariorum* in glasshouses (Burnett, 1949; Fig. 10.9). Cool weather is the ultimate cause of *Schizaphis graminum* outbreaks, as parasitoids become ineffective (Section **5.3.1.2(h)**). In the laboratory, the aphidiine wasp *Praon palitans* limits numbers of *Therioaphis maculata* at 21.0°C but not at 12.5°C (Messenger, 1964b). A like effect exists with two parasitoids in the dynamics of olive scales (Rochat and Gutierrez, 2001; Section **4.3.6**). In the field, ~75% of the variance in the efficiency of *Trichogramma minutum* to parasitize spruce budmoth eggs depends on temperature (Bourchier and Smith, 1996). Finally, in *Melitaea cinxia* and its parasitoid *Cotesia melitaearum*, asynchrony in diverse sub-populations due to different temperature regimes greatly effects the dynamics of both insects (van Nouhuys and Lei, 2004). While cold reduces the birth rate of *M. cinxia*, it abolishes enemy attack (Section **12.3.2.1**). From a mathematician's viewpoint, Schaffer (1985) accedes that if insect populations fluctuate widely, not having the stable equilibrium predicted by many models, it 'can *only* mean that external forcing in the form of climatic variation is paramount'.

The physical environment sets the rules for the biological games that are played. Species cannot exist outside upper and lower physical limits and operate inefficiently near them (Section **10.1.1**). This must be in mind when developing models (Remmel *et al.*, 2009): indeed some mundane models for forecasting pest outbreaks *depend* on accumulated temperatures above the developmental threshold. While the influence of temperature on growth is non-linear (Bonhomme, 2000), *day-degrees* (D°, Section **10.2.2.2**, q.v.) remain highly explanatory in Davidson and Andrewartha's (1948)

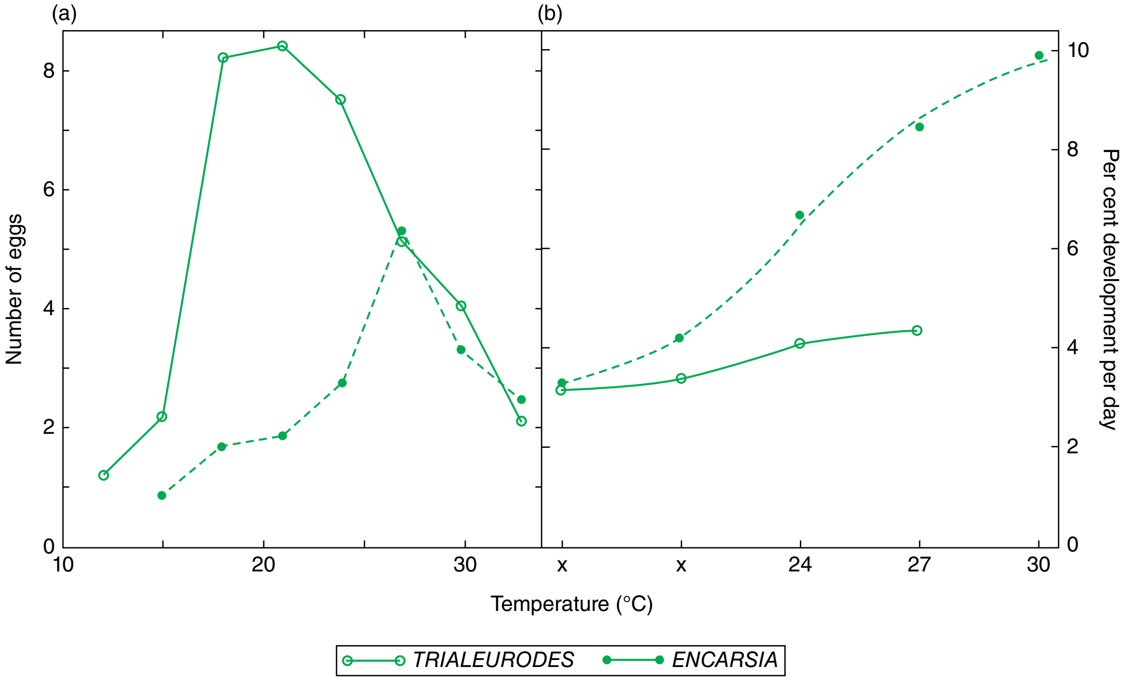


Fig. 10.9. *Trialeurodes* and *Encarsia* data from Andrewartha and Birch (1954) *The Distribution and Abundance of Animals*, Chicago University Press. p. 468. Note that higher temperatures tend to favour the parasitoid. Reproduced with permission.

famous study of thrips in roses. Obversely, *accumulated* low temperature has been shown recently to determine survival in winter. So we will usually consider the effects of physical factors on innate attributes *before* those of biotic ones, since the former commonly drive the latter.

In benign physical environments, we expect biotic factors to be more important than in harsh ones. Of course, this is because most invertebrates are inactive under harsh conditions. Even moderately low temperatures, low humidity and sunless weather cause a general decrease in insect activity. Predation by warm-blooded insectivorous mammals and birds, however, continues unabated. Insects can hide but they cannot run! By extension, as Thompson (1929) pointed out, and others have followed (Dobzhansky, 1950; Baker, 1970, Rathcke and Price, 1976; Greenslade, 1983; Schemske *et al.*, 2009), biotic factors should generally be more significant in the tropics and physical factors more so in temperate regions. This generalization, however, requires more research. Refer to the case above of several Caribbean solitary wasps. Indeed, in India, Beeson (1941) showed that density of the cossid borer *Xyleutes ceramicus* was limited by high rainfall (Section **4.2.1.2(k)**).

For biotic relationships also recall (Sections **9.6** and **10.1**) that the density of the population in which the individual exists is a unique factor. It affects the individual's innate attributes and, in turn, its RS, either via *primary intraspecific* effects or various *secondary interspecific* effects. The primary effects are competition, cannibalism (Sections **9.8** and **10.1**) and co-operation (Section **10.1.2**). Generally, the secondary effects operate through density-dependent mortality (Sections **10.2.3.7** and **10.2.3.9**) due to the action of enemies, although these may be ill-defined (Milne, 1962), inverse (Lessells, 1985; Stiling, 1987), or 'vague' (Strong, 1986).

Intraspecific competition often reduces the final size of females and their AF (Section **10.2.5.1**). But when it increases the time to develop (Section **10.2.2.5**) survival decreases due to the Williams' effect, a basic link between developmental rate and mortality. With longer development, a mortality factor *operating at a constant rate* will kill a higher proportion of the stage: a negative Williams' effect, and vice versa (Williams, 1966; Section **5.2.1.3(b)**). Of course, poor food itself, not the result of competition, may lead to negative Williams' effects. Then, small final size may limit dispersal (Section **10.2.4.1**), as in *Asphondylia* (Freeman and Geoghagen, 1987).

Here are some examples. Slow-growing winter moth larvae on sub-optimal food suffered high mortality from the tachinid fly *Lypha dubia* (Cheng, 1970). A like result occurred in the leaf beetle *Galerucella lineola* (Haggstrom and Larsson, 1995), in the leaf-mining agromyzid fly *Amauromyza flavifrons* (Uesugi, 2015) and is expected for many oligophagous herbivores (Section **10.2.2.2**). It may be hard, however, to separate *direct effects* from the food from secondary ones resulting from longer growth and increased mortality from enemies. For *parasitoids* attacking exophytic herbivores, Williams (1999) found evidence for negative effects in only 23% of cases, much less than that for *predators*. Parasitoids are less active at lower temperature, as in the case of *Encarsia* on whiteflies (Section **10.2.1**) and aphidiine wasps on cereal aphids (above). But temperature-independent predation rates may also well be inappropriate for insects. High density may also induce emigration (Nicholson, 1933; Section **10.2.4.6**), a further primary effect.

With sibling co-operation, positive effects on growth and survival may accrue. In the tropical butterfly *Chlosyne janais* the growth rate of sibling larvae doubles in big aggregations (Denno and Benrey, 1997) and probably reduces field mortality. Larval defences are improved in the moth *Hyphantria cunea* (Morris, 1976) and growth rate increases because feeding is facilitated (Lawrence, 1990). Congregation of non-siblings can also be advantageous, as when various bark and ladybird beetles respond to aggregation pheromones (Section **4.2.1.2(h)**). Here, mutual attraction is a proxy for patch and habitat location.

Density-dependent mortality may occur through successive generations of a species (*temporal density dependence*) but *spatial density dependence* also occurs (Richards, 1961; Freeman and Parnell, 1973; Walde and Murdoch, 1988; Hails and Crawley, 1992), places with high density having high mortality. While enemies often reduce survival, movement, particularly dispersal, may be affected (Section **10.2.4.8**). Interspecific competition usually has negative results (Section **9.8**), but *can be additive to intraspecific competition* (Connell, 1983). This may occur between larval winter moths and green tortrix moths (Section **5.2.1.4(g)**). It may then be hard to separate intra- from interspecific effects. Milne's theory of population (Section **11.2.2.4**) distinguishes intraspecific competition as being '*perfectly density dependent*', while interspecific competition is '*imperfectly density dependent*'. This distinction has more recent currency (Thompson and Grime, 1988; but see Berryman, 1991a). Interacting species may respond differently to a given environmental factor. Recall (Section **9.8**) that the *ecological efficiency* of different individuals and hence species varies. But there are diverse complexities, as follows.

Population density varies during an individual's life. Take the life track of a female *Pieris brassicae* (Section **5.2.1.4(l)**) surviving to old age. Firstly, it is an immobile egg in a batch. On hatching, and like many other caterpillars, behaviour changes as it grows (Tagawa *et al*., 2008). Next, it is one of a cohesive band of siblings whose numbers decrease with age and mortality. When older it is solitary, again at lower density. Aggregation when small does not lead to food shortage, but later when bigger it may well do so. Then it wanders off and selects a pupation site, producing a dramatic further decrease in density. Densities can be measured relative to the leaf (eggs, young larvae), plant patch (large larvae) or habitat (pupae). Then she emerges, flies off to become part of an itinerant population, mates, distributes several egg batches and dies many kilometres away. Its juvenile and adult ecologies are on different spatial scales (Levin, 1992); quite unlike cultured beetles in jars.

Cases of density-dependent dispersal of mature larvae (Section **1.5**), among many others, occur in *Acleris variana* (Section **5.2.1.4(g)**), cinnabar moths (Dempster, 1982), house flies (Section **7.4.2.3**) and *Euphydryas editha* (Weiss *et al*., 1988). In Jamaica, a group of *Pseudosphinx tetrio* (Sphingidae) larvae, that had been feeding on a 12.5 m^2 *Allamanda* bush, moved up to 16 m away to pupate, a potential 64-fold reduction in density, while *Papilio homerus* move up to 10 m onto adjacent trees (Garraway *et al*., 2008). On so complex a basis, we must view the effects of population density on movement, survival and other attributes. Most importantly, both *mortality and movement* can lead to reduced density (Taylor, 1984; Section **9.2**).

In time-series analysis (Section **11.3**), density is usually estimated at only one stage in the life cycle. Pascual and Levin (1999), in relation to models, discuss the complexities caused by changes in numbers and density, which we termed the number/density anomaly (NDA; Section **9.3**). Viewed simply, however, there is an optimal density or range of densities at a given stage that will maximize the RS of an individual (Fig. 10.10). Due to genetic differences this density may not be the same for all

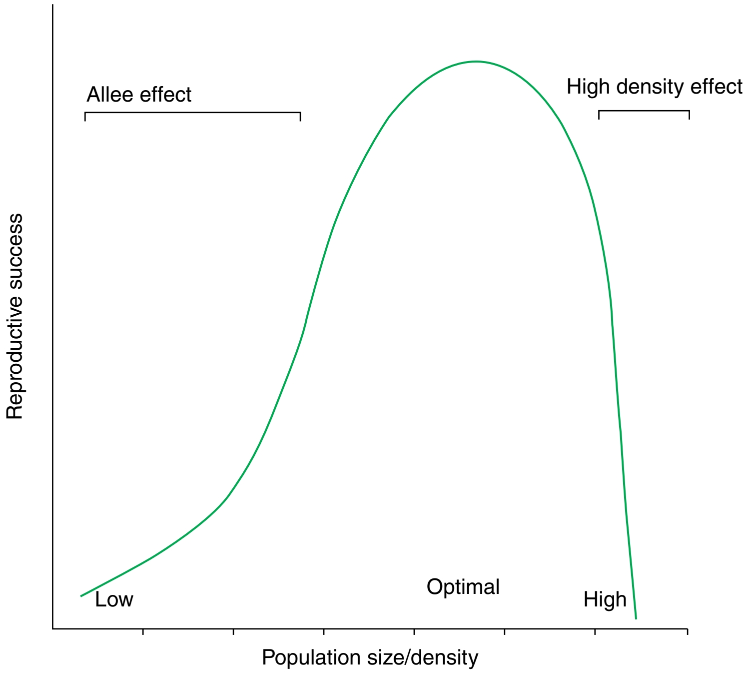


Fig. 10.10. Consequences of population size/density on reproductive success. Note the Allee effect.

individuals. Movement allows adjustment of density, as when the caterpillars above disperse when older, here reduced density ostensibly being advantageous.

Both physical and biotic interactions can be studied in the field or laboratory. While these may be difficult to inter-relate, they provide hard empirical data that can be presented in graphs and given statistical precision. However, Pielou (1981) remarks whimsically, ‘if you ask a statistical question you get a statistical answer’, one that may have several ecological interpretations (Stephens *et al*., 2006). Recall that correlation is not causation, and census data are often far from normal or even Poissonian (Taylor, 1961; Sileshi, 2006), with far too many zeros, and so need appropriate handling. But when statistical methods are used with adequate insight the results can be deployed in mathematical models, perhaps finally embodied in general theory. While such theory may be modified or even abandoned, well-founded data stand in perpetuity (Turchin, 2003).

Here and in Chapters 11 and 12 we consider insects in general, but select pest species where they provide pertinent examples. This should give a full understanding of insect pest ecology. While pests constitute only a small proportion of *all* insects (Section **9.4**), they are very relevant for us. Indeed, more is known about pest ecology than that of non-pest insects (Potts, 1990). Following selective sampling, however, we look at *all* the innate attributes in turn and in each case *several* of the environmental factors, choosing basic and/or interesting examples and others in which the factors act in concert or in sequence. We cannot consider all possible combinations. But again, not only do innate attributes interact with environmental factors, both may interact among themselves, while the concept of an optimal physical environment must be qualified. One optimal for growth may not be so for longevity or reproduction. Perfect environmental adjustment is mythical.

10.2.2 Development and growth

10.2.2.1 General introduction

The growth of an individual is an embryological process and, of course, not to be confused with the growth of the population of which it is temporally a member. Population growth can be seen as the *increase of a specific biomass*, transcending individuals and generations, ultimately forming an evolutionary lineage. With fast development individuals start to reproduce earlier, which is a critical component of the equations of population growth (Cole, 1954; Lewontin, 1965; Section **11.5.2.1**). But size is also a factor. Large females commonly lay more eggs than small ones, but if they take longer to reach maturity in continuously breeding populations this will offset this reproductive advantage. In univoltine species they may simply complete growth later in autumn. Longevity too is often higher in large individuals (Sokolovska *et al*., 2000).

Growth and development can be measured as the rate of change of an individual’s mass or as the duration of its development. Here physiology and embryology are basic to an innate attribute (Section **10.1**). But in insects only the juvenile feeding stages (nymphs and larvae) get larger, although eggs may absorb water, pupae lose mass and adults get heavier. Basically, eggs, pupae and adults just develop: their structure changes progressively. An embryo develops in the egg, an adult develops in the pupal case and in adults, gonads often develop. Flight muscles may grow or regress. In nymphs and larvae it is best to measure growth as increase in dry mass, or even nitrogen content, as a means of estimating protein gain, because water content can vary considerably. Of course, this means killing the experimental individual so that a sequence of measurements on it is impossible.

Eggs and pupae being non-feeding stages, however, usually lose mass during development, so to assess their rate of development one records the duration of the stage under known physical conditions. As above, both often exhibit external colour changes usefully marking internal changes. The duration of a juvenile stage can also be used to assess its rate of development. Adults may or may not take time to develop reproductive capability, house flies and clover weevils do, crane flies and gall midges do not. By definition, all juvenile stages take least time under ideal physical conditions unless they are in diapause. Males are frequently smaller than females and often emerge before them, the latter giving them better mating prospects (Section **9.8**). So, the final size of adults may have subsequent effects on thermal relations and their innate attributes: survival, movement and reproduction (Berry and Willmer, 1986; below). But rapid development may not result in the fittest individuals (Nylin and Gotthard, 1998) because reduced developmental control can produce asymmetrical adults. While asymmetry in *Drosophila* had been noticed long ago (Mather, in Thoday, 1953), research on its effects on insect fitness is recent. Suggestive data have been collected for the damselfly *Lestes viridis* (De Block and Stoks, 2007; De Block *et al.*, 2008). In the parasitic wasp *Trichogramma*, while wing size and shape are determinants of fitness in the field, alary asymmetry is not (Kolliker-Ott *et al.*, 2003). Of course, as in birds, wing shape affects flight performance and may vary between the sexes of a given species.

10.2.2.2 Growth: Physical factors: Temperature and insolation

Krogh's law states that temperature determines the rates of all biological processes. Internal temperature normally controls an insect's metabolic rate (MR) and, in turn, its growth rate. Although some juveniles bask (below) or use insulated shelters they are all poikilothermic (q.v.). So, ambient temperature controls growth rate, the length of the life cycle and, occasionally, their appearance. The duration of temperatures permitting growth, which may be measured in D° (below), must be enough to allow the insect to pass from the egg to the stage that diapauses during winter or drought, or total mortality ensues (Remmel *et al.*, 2009). Upper and lower limits exist to the temperature at which a *given individual* will develop, between which is the favourable range (Section **10.1.1**) for growth. To an extent this results from physical selection pressures on its ancestors. But if one investigates developmental rates in a large sample from the same population, the limits will be wider because of innate variability. With representative sampling these limits estimate those of the population. The lower limit is termed the lower developmental threshold (LDT). But rather, constant *sums of temperature* are needed to complete juvenile growth, a sum of D° or of effective temperatures (SET). Species from cool regions tend to have low LDT and high SET, those from warm regions the opposite (Dixon *et al.*, 2009). Growth rates have a significant genetic component. In *Pieris rapae* pupae at 25°C, 85% of the variance in developmental time is genetic (Gilbert *et al.*, 2010). Genes code for enzymes that have specific temperature optima (Heinrich, 1977).

Recall (Section **2.2.2.1**) that environmental heating greatly depends on soil temperature. In northern temperate regions after a long, cold winter, there will be a marked lag effect in spring, which will tend to be cool. Whatever the winter is like, mean temperatures in March are lower than those in September, although insolation is similar. So, if spring is late, the favourable season for both plants and insects will be reduced, females will have less time to oviposit, and juveniles may run out of time to complete development to the overwintering stage.

Developmental rate within the favourable range increases exponentially from the LDT until the optimum is approached (Fig. 10.11). There is a rapid decline from the optimum until an upper limit, where growth stops (Dixon *et al.*, 2009). In *Musca domestica*, development (egg to adult) takes 49 days at 16°C, 16 days at 25°C and ~9 days at 35°C (Service, 2000), but increases above this temperature. In phase one, thermal activation improves process efficiency, in phase two high temperature progressively inactivates some enzymes (Bonhomme, 2000). The optimum is much nearer the upper than the lower limit. But other factors (below) may constrain growth. Of course, growth depends on MR. This was traditionally expressed as a Q_{10} quantifying its temperature dependence over 10°C. But size also affects MR, scaling as the ¾ power of body mass. The effects of both factors may be incorporated in a general model of growth (Gillooly *et al.*, 2001; Savage *et al.*, 2004).

Within a species, development during diapause has a different relationship to temperature than that at other times. In *Austroicetes* (Section **5.2.1.1(e)**), diapausing eggs have an optimal developmental temperature of ~12°C, non-diapausing eggs develop fastest at ~35°C (Andrewartha and Birch, 1954; Fig. 10.12). In larval *Contarinia nasturtii* (Section **5.2.1.5**), a 3–4 month period of low-temperature (2–5°C) development is needed before pupation and normal growth can proceed (Readshaw, 1966). Overall, the tolerable ranges for many insects, essentially where growth can occur, are between 13°C and 29°C (Fig. 10.13). Field temperatures above the lower threshold for growth, determined in the laboratory, may be accumulated as D° (Section **10.2.1**). D° values have been used in other contexts, but are important in forecasting the time of pest attack. So, when 220 D° above a 9°C threshold has been reached in spring in Japanese apple orchards, *Pseudococcus* mealybugs can be sprayed (van Emden and Service, 2004), if better means are unavailable. Similarly, degrees accumulated *below* an appropriate threshold (say 0°C)

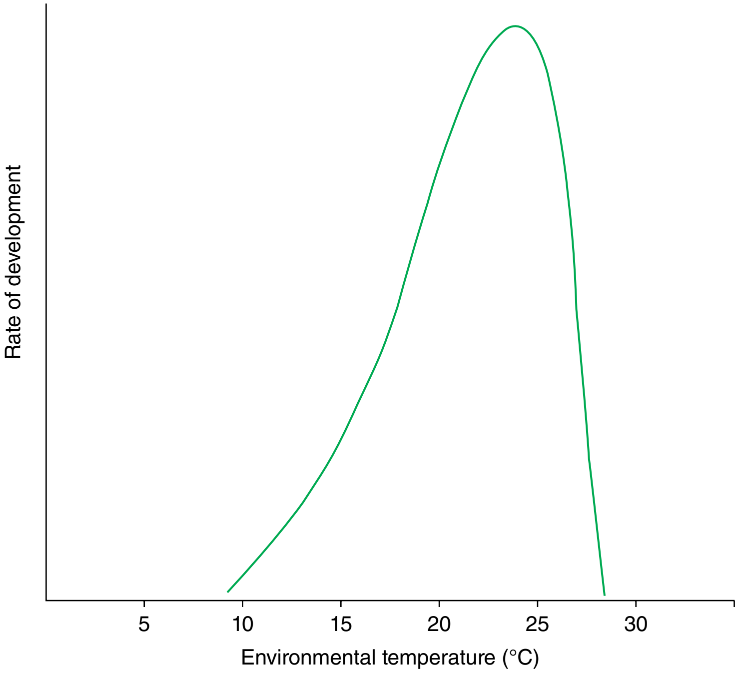


Fig. 10.11. Rate of development versus temperature – weight gain and duration of stage.

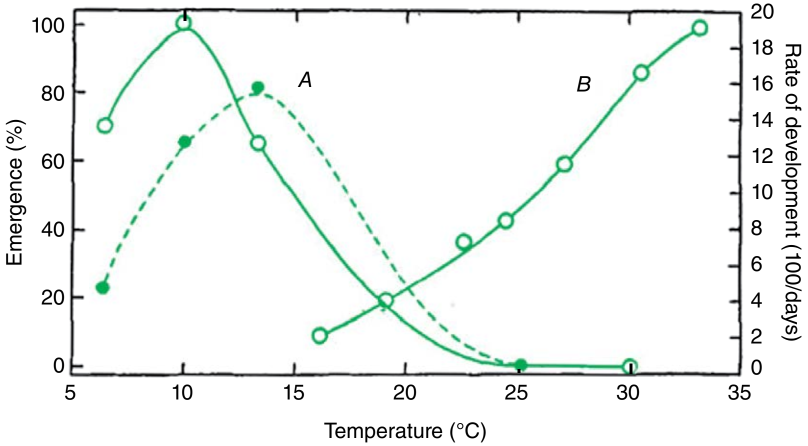


Fig. 10.12. Rate of development with respect to temperature of diapausing and non-diapausing eggs of the locust *Austroicetes.* From: Andrewartha and Birch (1954) *The Distribution and Abundance of Animals*. Chicago University Press, p. 66, Fig. 4.03, Reproduced with permission.

may be used in studies on survival and development of overwintering insects (Cárcamo *et al.*, 2009).

When they are below optimum temperature, diurnally active stages of many insects use their mobility to seek more favourable microclimates for development and growth (Section **10.2.4.2**). *Chorthippus brunneus* nymphs (Acrididae) in sunshine can raise their thoracic temperature by 4–5°C above ambient temperature, leading to faster development (Begon, 1983). Conversely, when insects are too hot they seek shade (Willmer, 1982). This interaction is between the innate attributes of development and movement with respect to temperature. But obviously it depends on there

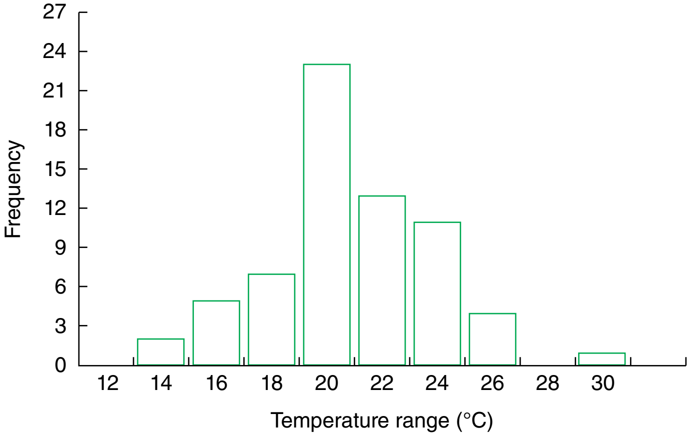


Fig. 10.13. Frequency distribution of the tolerable thermal ranges for a large sample of insects. These vary about a mode of 20°C and would be only slightly wider than the range for growth. From: Dixon, A.G.F., Honěk, A. *et al*. (2009) Relationship between the maximum and minimum thresholds for development in insects. *Functional Ecology* 23, 257–264. Reproduced with permission.

being sunshine. Of course, endophytic insects have much restricted options.

Apart from defensive functions against enemies (Section **10.2.3.5**), an insect's colour influences its ability to absorb radiant heat, which in turn affects growth. *Philaenus spumarius* (Cercopidae) has diverse colour and pattern morphs, eight of them being melanic (Berry and Willmer, 1986). Under radiant heat in the laboratory similar to that in the field, melanic bugs were ~1°C warmer than non-melanic ones, and large individuals (15 mg) were ~2°C warmer than small ones (8 mg). So growth to a larger size may influence thermal relations, the innate properties of size and colour jointly affecting the operation of a physical factor. In two montane psyllid bugs (Section **12.3.4.3**), the blackish species is found higher than its congener (Bird and Hodkinson, 2005). In the Rocky Mountains, the butterfly *Erebia magdalena* is sooty black (Emmel, 1991). In the UK, many noctuid moths are more blackish in the north than in the south (South, 1920/1923) and melanism is common in Alpine and Arctic insects (Sømme and Block, 1991; Leather *et al*., 1993). Melanic morphs of *Adalia bipunctata* survive winters better than red ones do. But Kuusijärvi *et al*. (2015) could find no function for the melanic morph in the beetle *Aphodius depressus*. Ambient temperature may change an insect's appearance by affecting its developmental pathways. Thus, the ichneumon *Exeristes roberator* developing at low temperature is melanic, those developing at a higher temperature are reddish (Thompson and Parker, 1928a). In the African satyrid butterfly *Bicyclus anynana*, temperatures of ~17°C during development induce the cryptic dry-season morph, but those >22°C induce the wet season one which has eyespots (Brakefield *et al*., 1996). However, bear in mind that melanism may have other functions including crypsis and protection from UV irradiance (True, 2003).

The relationship of insect growth to temperature is typically dissimilar in different orders, a further example of taxonomically related variation, here by having ostensibly different physiologies. In the same habitat, say the soil of a temperate meadow, the conditions are similar for all, but beetle larvae tend to grow more slowly than moth and fly larvae. Imagine the following. Wireworms (*Agriotes*, Coleoptera) take 3–4 years to develop, leatherjackets (*Tipula*, primitive Diptera) 1 year, cutworms (*Agrotis*, Lepidoptera) ~6 weeks (Section **3.2**) and house fly larvae (advanced Diptera, in dung) 2–3 weeks. While there are differences in temperature regime and food quality here, much of the effect on growth must be innate to the insect taxon. Such physiological variation affects the demographics of these pests, especially their rate of population increase (Cole, 1954).

Because of far greater insolation (Section **2.2.2**) and hence higher ambient temperatures in the tropics, most insect development there is faster than in related species in higher latitudes. The tropical mosquito *Aedes aegypti* (Section **7.3.2.4**(**e**)) may develop from egg to adult in ~10 days, while *A. punctor* on a Scottish moorland has but a single annual generation (Packer and Corbet, 1989), despite the fact that summer days there are long. So tropical insects usually have short life cycles, several generations per year and a potential for a high rate of population increase. *Laodelphax striatellus* (Delphacidae) is bivoltine in Sweden (60°N) but has 12 annual generations in Israel (32°N) (from Denno and Roderick, 1990). In cool climates, winter calls a halt to the life cycles of most insects and many enter diapause (Section **10.2.3**), although it is usual for those in more buffered environments, such as the soil and in water masses, to be fairly active if it is not too cold. Thus, in Michigan, USA, the soil-living larvae of the weevils *Polydrusus*, *Phyllobius* and *Barypeithes* grow appreciably during winter (Coyle *et al*., 2011). In the UK, the semi-aquatic larvae of *Tipula luteipennis* grow measurably from October to March (Freeman, 1967b). But in high montane and polar environments, temperatures are too low for most species to complete development in one season (Greenslade, 1983). In an extreme case, the moth *Gynaephora groenlandica*, which feeds on Arctic *Salix*, may take 14 years to develop, its juveniles diapausing repeatedly. But apart from the direct survival value of diapause, it synchronizes the life cycle in relation to climate (Tauber and Tauber, 1981).

Where diapause occurs irregularly and/or on the edge of distribution, incomplete development in cool seasons causes mortality of a maladapted stage (Section **12.3.4.3**). Then a harsh season results in slow growth and late emergence of adults, who have less time to lay eggs. When *Masonaphis maxima* (Aphididae) was displaced experimentally to a cooler region, it had insufficient time to produce overwintering eggs (Gilbert, 1980). This effect also occurs in *Neophilaenus* (= *Philaenus*) (Cercopidae) on high moorland (Whittaker, 1971) and may apply in the montane bug *Craspedolepta* (above; Bird and Hodkinson, 2005). Extended development due to cold may result in a negative Williams' effect, as in *Limenitis* (= *Ladoga*) *camilla* (Nymphalidae), where increased avian predation occurs (Pollard, 1979). In the seasonal tropics, diapause is often a means of enduring drought or excessive wetness, that is, times when essential food, like a plant's seasonal flowers or fruits (Section **6.1**), are absent. Drought there is comparable to cold at higher latitudes, and may limit distribution (Tauber *et al*., 1998).

Cosmopolitan insects with distributions reaching from the tropics to high latitudes generally have different *innate* growth rates in relation to temperature in the two regions, their populations being so adapted. Even on a limited scale, when *Dendroctonus ponderosae* (Section **4.2.1.2**(**h**)) from central Idaho (45°N) and southern Utah (37°N) in the USA were reared together at ~21°C, the northern beetles had a much shorter mean time for development (61.7 days) than southern beetles did (96.3 days) (Bentz *et al*., 2001). Similar variation occurs in *Bactrocera* (= *Dacus*) *tryoni* (Tephritidae) from different latitudes in Australia (Andrewartha and Birch, 1984). The temperature at which individuals develop also influences their final size (below), but interactions exist with food quality and supply, and reproduction is also affected (Section **10.2.5.3**). After controlling for size, the MRs of temperate insects at a given temperature are normally greater than those from the tropics (Addo-Bediako *et al*., 2002). Oddly, there are differences between insects from northern and southern hemispheres (Section **2.2.3.2**).

Insects developing at temperatures less than optimum for growth, but within the favourable range (Section **10.1.1**), often produce larger adults. *Trichoplusia ni* (Shorey *et al*., 1962), the whitefly *Bemisia*, the midges *Culicoides furens* (Linley *et al*., 1970) and *C. variipennis* follow this pattern. So does the sub-tropical mosquito *Toxorhynchites rutilus*, but here photoperiod also has an effect (Lounibos *et al*., 1998). But when Colorado beetle larvae feed at low temperatures, adults are smaller and less fecund (Lyytinen *et al*., 2009). In *Calathus melanocephalus* and *Pterostichus versicolor* (Carabidae), females given abundant food grow to a smaller size at 12°C than at 19°C (van Dijk, 1994). These laboratory beetles were much smaller than those sampled from the field, possibly because the quality of their food was deficient. *Phyllopertha* (Section **3.2.1.2**(**b**)) in pastures grows to a larger size at higher temperature (Laughlin, 1963), and so does another beetle, *Atomaria linearis* (Cochrane and Thornhill, 1987). Beetle growth with respect to temperature may be exceptional, again, taxonomy having outcomes for physiology. Even so, for the moth *Malacosoma* (Section **5.2.1.4**(**e**)) pupal weights are greatest at 27–30°C, near the optimum for growth (Frid and Myers, 2002). More research is needed here.

10.2.2.3 Growth: Physical factors: Precipitation and moisture

An individual's rate of development is influenced by humidity if it becomes desiccated or bloated with water. Its metabolism slows due to ionic imbalance. As with temperature, an external physical factor produces a physiological outcome. In nature, of course, temperature may have an effect at the same time. The mobile stages of insects (Section **1.2**) can offset desiccation by seeking and finding free water, but immobile ones cannot do so (Section **10.2.4**). Some species develop faster the higher the humidity. Others have an optimum of ~75% RH, with the rate slowing nearer to saturation. In soil, *Contarinia nasturtii* (Section **5.2.1.5**) larvae become quiescent during drought, and construct spherical cocoons that are distinct from the ovoid ones made for pupation (Readshaw, 1966). But in general the nature of the soil, whether it is well drained or not, an edaphic factor, affects this. Hot, dry weather induces diapause in *Heliothis fletcheri* (Section **6.2.1.2**(**h**)), although here temperature, not humidity, may be the causal factor. A few insects such as the lucerne 'flea' *Sminthurus* (Collembola) absorb too much water in saturated air, becoming bloated with excess. Finally, some insect eggs during diapause, like those of plague grasshoppers (Section **5.2.1.1**), are extremely resistant to desiccation and uninfluenced by dryness except in the very long term, but they respond to wetting by initiating the final stages of development.

Some larvae are unaffected by humidity since their food contains abundant water, as in folivorous caterpillars in humid forests. Water is absorbed in the hindgut and the faeces (frass) are quite dry. But if they defoliate a tree insolation increases, humidity falls and because food becomes scarce they may desiccate. Sequential effects like this run through autecology (Section **10.1**), where we saw how rainfall variation affects foliage production. This is marked in the seasonal tropics (Sections **2.2.3.2** and **5.2.1.1**(e)), leading to effects on the growth and phenology of such folivores (Wolda, 1978). The developmental rate of pupae is often affected by atmospheric humidity as they are sessile and non-feeding, although those having a long duration may be very resistant to water loss. In moths and ichneumons, the cocoon helps to maintain favourable humidity. In the diprionid sawflies (Section **5.2.1.3**(e)), which often live in harsh physical conditions on conifers, the cocoons have a double wall. *Trypoxylon palliditarse* (Section **12.4**) also makes double-walled mud cells, a behaviour that thwarts parasitoids.

10.2.2.4 Growth: Biotic factors: Conspecific organisms and population density

Each individual in a population is influenced potentially by contact with others (Sections **10.1** and **10.1.2**), this being part of Richards' definition of population (Section **9.5**). Contact frequency is usually a direct function of population density (but see Lloyd, 1967). The resulting outcomes may be positive or negative for each individual, but there are different optimal densities for the various innate attributes (Section **10.10**). Recall that density, alone among biotic factors, operates predictably and unfailingly on its members. While this does not abolish a role for individual variation, Allee (1932) showed that low density could be disadvantageous, the 'Allee effect' (Section **9.8**). Where individuals live in groups, often assisting each other in some way, there is an optimal group size, an 'Allee threshold', below which negative effects begin to accrue. Thus, some stored-products beetles are better able to chew into grain at moderate densities, so enhancing their growth (Andrewartha and Birch, 1954). But the Allee effect has other outcomes (Sections **10.2.3.7** and **10.2.5.6**). For growth, insects eating living plants may either decrease or increase quality. The former is more frequent, but there are several cases of the latter. Thus, the aphid *Elatobium abietinum* feeding on spruce needles causes chlorotic areas in which amino acids have enhanced quality (Kloft and Erhardt, 1952, in Awmack and Leather, 2002). One suspects similar effects where juvenile siblings feed together, although their defences and hence survival may also be improved. Indeed, growth rate often has consequences for survival through the Williams' effect, and while we deal primarily with growth here, we make brief reference to this other attribute. For growth, however, high density normally has negative effects through food, especially via competition for high-quality, or simply sufficient, food (Section **10.2.2.5**). Faecal material can pollute it, less obviously feeding by one individual on a living plant may induce its defences, reducing the growth of others. Such negative outcomes in culture include the classic results of Nicholson and Bailey (1935) on blow flies and on pests of stored products (Crombie, 1947; Park, 1962; Utida, 1972;

Section **6.3.1.2**). Scarce or polluted food reduces growth rate and then survival, final size and AF (Section **10.2.5.2**). We now consider additional aspects of the influence of food on growth.

10.2.2.5 Growth: Biotic factors: Food

The basic properties of food are quantity and quality (Section **9.8**). Both have positive and negative components (Section **2.4.2**). A lack of positive components and a high level of negative ones, both reduce quality (Berenbaum, 1995). In Africa, the flood-plain grass *Cynodon dactylon* provides an example. As flooding subsides, extensive 'lawns' of this plant develop. With drying out these areas decrease, but as the grass becomes stressed for water its amino-acid levels increase, improving its quality for locusts (White, 1976; Section **5.2.1.1(a)**).

While the effects of food start at the physiological level, primarily with growth, there are usually outcomes for survival and AF. Deficient quantity and quality give extended development and a Williams' effect. Fewer individuals survive and become either pupae or adults. Slow growth may cause the focal species to 'run out of time' (Section **10.2.2.2**) and enter a physically unfavourable season. Slow growth (physiological) translates into reduced RS (a population result). Plant food quality for herbivores is affected by innate and external factors. Thus, some individual plants produce higher levels of defensive compounds than others (Section **2.4.2**). Then, C_4 plants (q.v.) may be innately less nutritious than C_3 ones (Caswell and Reed, 1975). Also, plants grown in fertile soil or crops supplied with fertilizers, or stressed by drought (above), often provide superior food.

Nymphs and larvae need food for growth, maintenance and movement, but they also store nutriment for future use. Physiological decisions must regulate this apportionment (Fisher, 1930; Section **9.7**). Apart from stores carried through in the fat body from their juvenile phase, adult females in many species, for example anautogenous mosquitoes (Danks, 2007), Parasitica (Flanders, 1953; Jervis and Kidd, 1986) and cyclorrhaphan flies, need food for ovarian development (Section **10.2.5.2**). They also need it, often in large amounts, as flight fuel, especially during any redistribution (Taylor and Taylor, 1977; Walter, 2003) and for reproduction, mainly in finding mates and multiple oviposition sites (Section **10.2.4.7**). Food quantity and quality inter-relate, so a surfeit of one may compensate for a lack of another (Section **10.1**). Even so, essential nutrients must be present (see below). In herbivores the quantity of food processed is limited by their ability to ingest, assimilate and detoxify it, less often by its availability. As living plant food varies in quality, herbivores usually select superior items, such as young leaves over mature ones. They employ their evolved *behaviour* to optimize this biotic factor. But *Dicranotropis hamata* (Delphacidae) has high ingestion rates when leaf nitrogen is low and vice versa when it is high (Waloff, 1980). These bugs also select plant parts high in nitrogen. The larvae of two beetles and a moth prefer leaves at a 95% expansion, often those in positions three to five from the shoot apex.

In oligophagous herbivores a preference may exist for the species the parents fed on (Section **9.10**), although induced preference (i.e. through shortage) can mask innate behaviour (Jermy *et al.*, 1968). Recall that better food reduces the time for development or increases the size of the mature juvenile, or both, so giving higher RS. But herbivores and carnivores often choose *a variety* of foods: there is *dietary self-selection* (Waldbauer and Friedman, 1991; Singer and Bernays, 2003; Stout *et al.*, 2006), in turn increasing growth and RS. Plant food is often poor because it is deficient in nitrogen (White, 1993; Section **2.4.2**). Angiospermous leaves contain only 1–5% nitrogen (dry weight) and those of gymnosperms rather less (Mattson, 1980b; Speight *et al.*, 1999), a level usually decreasing as they age. Highest levels are found in actively growing tissues, but the form in which nitrogen enters the insect's digestive system is key (Chen, 1966; Cockfield, 1988). Free amino acids are digested better than complex proteins. A particular suite of *essential amino acids* is always needed. These possess the carbon skeletons that an insect cannot synthesize *de novo* (Gündüz and Douglas, 2009). For sap suckers, amino-acid levels are usually <<1%, grossly unbalanced for them, and extremely low in xylem. So all herbivores must process a relatively great weight of food. The use of nitrogenous fertilizers to enhance crop yield can, unfortunately, enhance pest nutrition (see above). Other components of food such as phosphorus and various trace elements are essential (Polis, 1999). Groups of some adult butterflies, especially males, may be seen imbibing water at muddy puddles in Amazonia (personal observations), where nutrients are generally in short supply. One view is that they seek to replace sodium ions (Boggs and Jackson, 1991).

Most juveniles feeding externally on plants above ground mature in a few weeks if inimical factors do not kill them. Pests underground or in woody stems often take much longer (Section **3.2.1.2**). While food is largely a biotic factor, when it is a plant both its quantity and quality are affected by the physical environment, again there is a *sequence of influence* firstly physical, secondly biotic. Thus, in wet years balsam firs produce few male cones, the food of choice for spruce budmoths (Section **5.2.1.4(c)**). Food quality influences the survival of young locust nymphs (White, 1976). Due to preceding rainfall patterns the grasses they eat may become nitrogen deficient and >90% die. Food quality for herbivores also changes predictably during the season: in trees defensive compounds usually build up with time (Feeny, 1970; Forkner *et al*., 2004; Section **2.4.2**). But in deciduous forests two types of leaf production exist (Niemala and Haukioja, 1982). In the *oak type,* all leaves are produced in spring, and develop protective tannins as they mature. In the *poplar type* new leaves are continually produced during summer, so good food is always available for insect growth. Then, food plants may senesce early in the year before some of the larvae eating them have matured (Cappuccino and Kareiva, 1985). So they run out of time.

Poor quality of food, then, results in large quantities being consumed. So the *conversion efficiency* (CE), that is, the efficiency with which the consumer converts a given mass of food into its own body mass, is linearly related to food quality measured by nitrogen content (Mattson, 1980b), as in *Pieris* larvae (Slansky and Feeny, 1977). CE values vary from <1% for many phytodetritivores (Section **8.2.4**) to >50% for larval solitary bees provisioned with ‘bee bread’, a pollen/nectar mixture. Consumers of nutritious plant parts (seeds and storage organs) and carnivores occupy intermediate positions on this scale. In *Sceliphron*, larvae feeding on provisioned spiders have a CE of ~26% (Freeman, 1981c). Although in general it is more efficient to harvest nutritious food, this is usually scattered and localized, requires higher ISC to find it (Section **10.2.4.1**) and is often the focus of competition.

All living food, namely living organisms, evolve defences. For plants these involve the mechanisms noted in Section **2.4**. There is a variety of physical and chemical deterrents, some permanent, others induced by attack. Feeny (1970) suggested that the low nutritive quality of foliage is itself an evolved mechanism of defence, but what hurts the herbivore does not necessarily help the plant (Moran and Hamilton, 1980). Perhaps a herbivore would destroy *more of a plant* when the latter defends itself, a defence that in any case should bear a cost. Organisms are selected by increasing their own RS, not by decreasing that of others. But the link between slow plant growth and its degree of defence can be strong (Grime, 1974). Plants hurt herbivorous larvae diversely, often by slowing their growth, with a negative Williams’ effect ensuing and fewer large larvae, the most voracious stage, surviving. Smaller adults and lower AF can result (Moran and Hamilton, 1980; Haukioja, 1990). In the long term, herbivores should seek other foods. But Crawley and Nachapong (1984) found no deleterious effects on cinnabar moth larvae developing on regrowth foliage of their ragwort food plant, which contains high alkaloid levels. Probably they have evolved effective pathways to detoxify them.

There are two ostensibly different hypotheses of food choice by herbivores: the *plant stress hypothesis* (White, 1976, 1993) and the *plant vigour hypothesis* (Price, 1991). Stressed plants, typically during drought, show increased amino-acid levels and so improved quality, while their ability to synthesize defensive metabolites may be compromised (Rhoades, 1985). Price marshals evidence that fast developing plants or plant organs are items of choice for many herbivores, which is certainly the case in Room *et al*.’s (1989) study of beetles devouring the aquatic weed *Salvinia* (Section **8.2.3**). However, the dichotomy collapses into the general proposal that herbivores endeavour to choose the plant food that best suits their present requirements, either by eating stressed plants or vigorously growing ones should these be available.

Choice by *Melanoplus differentialis* (Section **5.2.1.1**) presents an intriguing insight into food quality. Nymphs were fed *Helianthus annuus*, when they preferred damaged, wilted, senescent or diseased leaves to healthy ones (Lewis, 1984) – as White would predict. Sibling groups of females fed a mixed diet of normal and damaged leaves, with normal leaves as control, had faster development, reached a mean mass of 2.18 g as opposed to 1.90 g, and a mean AF of 589 instead of 489. *Spodoptera exigua* grow better on diseased groundnut plants than on healthy ones (Section **5.2.1.4(j)**). The larvae of some *Sterrha* spp. (Geometridae) prefer withered to fresh foliage. Those of several large forest moths eat old leaves, which have limited value to the tree. These may be co-evolved situations in which the insect removes old or infected food without affecting future production, but the phenomenon seems not to be widespread. In contrast, some senescent foliage delays maturity in desert locusts (Ellis *et al.*, 1965). The mechanisms here are most likely complex.

Indeed *variety*, rather than senescence, can improve quality. Other *Melanoplus* spp. and other grasshoppers consume food in variety (Waldbauer and Friedman, 1991). Older larvae of *Orygia* (Section **5.2.1.4(f)**) have higher fitness on an age mixture of balsam foliage (Johns *et al.*, 2009). Two cutworms, *Polia oleracea* and *P. dissimilis*, need a variety of plants, growing less well on single, even preferred species (Merzheevskaia, 1961, in Jermy *et al.*, 1968). Gypsy moth larvae often move from one to another tree species. In the laboratory pupal mass varied by an amazing *factor of over five* on different combinations (Barbosa *et al.*, 1986). Larvae on a willow oak/sweet gum diet produced pupae of mean mass 2.45 g and mean AF of 941. By contrast, for those fed a black oak/red maple diet these values were only 0.43 g in mass and 71 for AF.

As in *M. differentialis*, other organisms attacking a plant affect its quality for a herbivore. Fungal endophytes (Saikkonen *et al.*, 1998) live symbiotically in most plants, and may well affect their quality as food. There are positive and negative effects on RS in these interactions (Stout *et al.*, 2006). Positive effects occur when the aphids *Rhopalosiphum padi* and *Sitobion avenae* feed on cereals infected with Barley Yellow Dwarf Virus. Similarly, when *Apion onopordi* feeds on the thistle *Cirsium arvense* infected with the rust fungus, *Puccinia punctiformis*, that is transmitted by these weevils, their RS is increased. But larvae of the butterfly *Melitaea cinxia* abandon leaves of *Plantago* infected with powdery mildew, and when the beetle *Cassida rubiginosa* feeds on *C. arvense* infected with the fungus *Phoma destructiva* its RS is greatly reduced (from Stout *et al.*, 2006).

For carnivores and parasitoids, with better and less variable food quality (plants are built largely of carbohydrate, animals of protein), it is more common to find that supply is limited by the searching power of the individual in relation to the distribution, density and the defences of their victims. Herbivores often experience a *qualitative* deficiency in their food, carnivores a *quantitative* one (White, 2001). But even some predatory insects avoid poor quality prey and we recall that those insects having warning coloration usually contain defensive compounds (Section **5.2.1.3(b)**), just as plants do.

Consumers of phytodetritus process it in large quantities as it is poor quality, although this is improved by the ingress of fungi and bacteria that they also eat. While it is unreactive to being eaten it may still have some defences left over from its living past. Plant detritivores typically employ symbiotic microbiota to pre-digest it. While some such insects (wireworms, crane fly larvae) also eat living plant roots their period of growth is generally long (Section **3.2.1.2**). By contrast, dead food of animal origin is, at least initially, nutritious, and the development of insects eating it consequently rapid. While detritus is usually defined inclusively (Lincoln *et al.*, 1982), recall (Section **8.2.4**) that there are three types of increasing nutritive value and localization: *phytodetritus* of plant origin, *coprodetritus*, especially mammalian and avian dung, and *zoodetritus* comprised of dead animals.

But the consumption of dead food does not reduce its rate of supply until, of course, it is all used up. With living food, however, consumption reduces this rate (Andrewartha and Birch, 1954). When a few caterpillars feed on a big tree, the effect is trivial (Section **10.1**). But if, say, 20 Colorado beetle larvae are feeding on a small potato plant their attack slows its growth rate so that at some point more is consumed than produced. Hence, plant growth becomes negative and this may result in resource competition, with negative outcomes on growth rate, survival and final size of the adults. In population terms, a similar thing can happen when predatory insects feed on a group of prey such as aphids: predation reduces the rate of their increase, which eventually becomes negative, and this may lead to food shortage for the aggressors.

When considering the likelihood of competition for food (Section **9.8**) one must determine if its supply is relatively short. Again, physical factors have primacy because at lower temperatures and unfavourable humidities poikilothermic insects, unlike birds and mammals, eat less. For temperate phytodetritivores there is often a vast pool of organic material in the soil, of which they use very little. Food is normally never in short supply or the object of competition. The annual litter fall (dry) in a Canadian broad-leaved forest is given as 4.3 tonnes/ha (Bray and Gorham 1964; see below for the tropics). Despite much discussion and contrary opinions (Murdoch, 1966b; Tilman, 1987; Denno *et al.*, 1995), I believe this situation to be true for a great majority of herbivorous insects, as do Andrewartha and Birch (1954), Thompson (1956), Hairston *et al.* (1960), Lawton and Strong (1981), Shorrocks *et al.* (1984), Jermy (1984), Wellings (1987), Begon *et al.* (1996) and Lawton (1999). It is the so-called 'green world hypothesis'. Bear in mind that most of these herbivores are scarce (Section **9.4**). On a recent walk in June in Hertfordshire I passed ~10 km of stinging nettles along the paths, the food of *Inachis io* and *Aglais urticae* (Wiklund, 1984), two common butterflies. June is their larval period, but I found not even a single batch of their obvious larvae. Their world was green and unchewed, much of it growing actively, in the sheltered situations they prefer and superabundant for their needs had they been there. Four such batches many kilometres apart are the most I have seen on such walks over half a century. They consume the same food, but the offspring of different adults never meet. While adult males may compete for territories, competition for food is unimportant. Only a few of the moths of North American hardwood trees ever causes noticeable defoliation (Hunter, 1991), a situation expected from the form of the species-abundance curve (Strong *et al.*, 1984; Section **9.4**). Emlen *et al.* (2005) show in great detail that male armaments in the dung beetle Onthophagus, used in competition for females that are on resources already, are more developed in species with dense populations. Only in such cases does competition for resources drive selection.

Most workers seek potentially competitive situations and study abundant species, producing a biased view (Lawton and Strong, 1981; Connell, 1983). Similarly, those investigating the strength of natural selection usually seek demonstrative cases (Kingsolver *et al.*, 2001). But when one studies a landscape (km^2), not just a patch (m^2), the greenness of the world is obvious (Polis, 1999), even though such an area has a fauna of many thousand herbivorous species. Thus, for all insect folivores of Panamanian forest, Leigh (1975) estimated that <300 dry kg/ha of leaves had been destroyed by insects out of an annual leaf drop of some 7 dry tonnes/ha (<4.3%). Although during peak periods as much as 14% defoliation has been recorded, Nair (2007) estimated only ~2% annually for trees in Kerala, India. While it is true that herbivores prefer specific plant parts, they cannot compete if they are metres apart. Even for all herbivores, not insects alone, Polis and Strong (1996) state that 'about 10%' of plant production on land is consumed, although there is considerable variation. Hence, I would urge devotees of the universality of competition in folivorous insects to take a walk and take a look.

But food may be intrinsically scarce, as are mammalian carcasses and rare plants. If individuals have good powers of searching and finding, however, as blow flies do (Sections **7.4.2** and **10.2.4.1**), competition for food may take place even at a low landscape population density: the number of eggs they lay often far exceeds the carrying capacity (q.v.) of a carcass (Del Bianco Faria, 1999). Although these flies may be sparse relative to the landscape, the larvae are often dense on the food patch. While severe competition exists within and between blow fly species, the fragmentation of the food resource promotes co-existence in the landscape (Hanski, 1987). Scarce plants have fewer insect species attacking them than common plants do (Southwood, 1961). Then, within the confines of *Asphondylia* galls, competing ectoparasitoids consume not only midge larvae but also each other: the end result is again cannibalism (Freeman and Geoghagen, 1989). There is also a good case for competition among mosquito larvae living in containers (Juliano, 1998). In all, when competition for food exists, it is more severe when the latter is nutritious and localized than when it is poor and diffuse.

10.2.2.6 Growth: Biotic factors: Other organisms: Symbionts

First, leguminous plants, often growing in poor soils, employ endosymbiotic, nitrogen-fixing bacteria or bacterioids such as *Frankia*, *Rhizobium* and *Bradyrhizobium* in special root nodules (Sprent *et al.*, 1987). Other such microbiota include *Sinorhizobium* and *Azorhizobium* (Werner *et al.*, 1992). Many new, specific proteins are produced in such nodules. Some other plants associate with blue-green algae (Mattson, 1980b). Then, several free-living, nitrogen-fixing micro-organisms (*Brosimum*, *Qualea, Schizolobium)* live on plant surfaces (Reed *et al.*, 2011). Symbiotic mycorrhizae often link plants physically, while others parasitize each other's roots (Atsatt, 1983, in Polis and Strong, 1996; van der Heijden *et al.*, 1998). Some 80% of all plant species are affected, and especially their phosphorus metabolism. Other fungal endosymbionts are little known (Omacini *et al.*, 2001). For entomology all of them probably have nutritional and other outcomes for the insects feeding on such plants, even on their parasitoids, and hence on selection. The ecological web is indeed diverse.

Second, numerous insects have co-evolved with microbiota to mutual benefit (Smith and Douglas, 1987; Dillon and Dillon, 2004; Feldhaar, 2011; Moran, 2015). Insects get better quality food and, in turn, achieve increased growth rates. Symbionts often defend their hosts from pathogens, detoxify plant allelochemicals (Section **2.4.2**) such as flavonoids, tannins and alkaloids, and gain mobility and a protected living space. They are probably universal in the insectan gut, but are more diverse in wood and litter-feeding insects. Hosts often have specialized diverticula, where pH and redox potentials are adjusted, in which the symbionts concentrate. Unfortunately, the study of symbiotic microbiota is hampered since their large majority cannot yet be cultured. Even so, most plants and insects are co-evolved with such symbionts. Feldhaar even suggests that the focus of evolution is not simply the individual but the *holobiont* (q.v.), the individual plus its symbionts (Section **9.6**).

Termites (Section **4.2.1.1**) employ a variety of microbes to degrade their cellulose-rich food. Bacterial symbionts, including *Acinetobacter, Bacillus*, *Pseudomonas*, *Pseudotrichonympha* and *Streptomyces*, increase the nymphal growth rate. As they live within the termite's gut they are lost at ecdysis. Thus, the nymphs must re-infect themselves from their neighbours at the start of each instar, an imperative integrating their social organization (Thorne, 1997; Nalepa, 2015). The main drawback with wood as insect food is that it has too much carbon and not much nitrogen. In some termites, special symbionts remove some carbon as methane and others fix atmospheric nitrogen, rather like *Nitrobacter* in the root nodules of legumes. While soil nitrogen may be short the atmosphere is comprised of ~80% of it, a vast pool which organisms in perpetuity have been unable to exploit in any extent (Dillon and Dillon, 2004).

Most aphid species (Sternorrhyncha) house the bacterium *Buchnera* in special organs or *bacteriomes* in their haemocoel, within which they inhabit special *bacteriocytes* (Wilkinson and Douglas, 1995; Douglas, 1998; Oliver *et al*., 2008). Such endosymbionts are either *obligate*, providing their host with essential food stuffs, or *facultative*, when apparently they do not (Baumann, 2005). The former is transmitted maternally via the ovary. Aphids stripped of their bacterial flora with an antibiotic have an upset amino-acid balance in their haemolymph and a reduced rate of growth, suggesting that antibiotics translocated in the plant's phloem, rather like systemic insecticides (Section **13.2.3.1**), might provide a 'green' means of control.

The Auchenorrhyncha also possess a variety of symbiotic microbes. The bacterium *Sulcia muelleri* may have lived in these bugs from the Permian, occupying large, paired bacteriomes in the abdomen. In those specialized xylem feeders, the sharpshooters, the bacterium *Baumannia* appeared in the Tertiary. *Sulcia* synthesizes amino acids and *Baumannia* provides vitamins (Moran, 2007). The Psyllidae (Section **5.3.1.2(b)**) contain the obligatory symbiont *Carsonella ruddii* (Baumann, 2005). Moran suggests that several symbioses are so intimate that some bacterial genes have been transferred to the genome of the host and their products passed back to the bacterium. We may well not be the first to achieve genetic engineering!

Other insects whose food is enhanced by symbionts include cockroaches, wood wasps, bees, leafcutter ants and beetles including chafers, woodworms, weevils and bark beetles (Section **4.2.1.2(f)**). The beetles are generally symbiotic with a diversity of fungi contained in *mycetocytes*. The larval guts of those species of crane fly that feed on plant detritus and rotting wood have large, variously developed diverticula containing diverse microbes (Freeman, unpublished data). Some blood-sucking insects, such as lice, bed bugs, tsetse and Pupipara, contain symbiotic microbes too. In general, insects that consume lots of poor quality food employ symbionts. Even so, honey bees and bumble bees are associated with several bacterial species in their guts (Koch and Schmid-Hempel, 2012; Moran, 2015). These include *Gilliamella apicola* and *Snodgrassella alvi,* which have nutritive roles and also protect their hosts against pathogenic trypanosomes.

10.2.3 Survival and diapause

10.2.3.1 General introduction

While survival is a demographic process and diapause a physiological mechanism, they are coupled here to express the latter's related importance. Recall the role of adaptive insect physiology at the interface of environment and individual. Essentially, diapause improves and/or permits survival during harsh seasons, an example of phenotypic plasticity (Birch, 1960). It is induced by the external environment and mediated by a diapause hormone from the brain (Fukuda, 1951; Sonobe and Keino, 1975, in Mousseau and Dingle, 1991). Survival is a less complex attribute to consider than either growth or fecundity since an individual either lives or dies. Remember that death may have environmental or genetic causes. Since all individuals ultimately die we are concerned largely with mortality before or during reproduction, as this has more impact on population processes, including their genetic aspects. Starting with the egg, 95–99% of herbivorous individuals commonly die before reproductive age (Hawkins *et al*., 1997), so selection can be very powerful. Rarely, mortality is much less, often resulting in rapidly increasing numbers, sometimes outbreaks. But in other species, like *Melittobia*, it simply results in better scanning of the landscape for new resources.

The differential mortality of individuals is an ecological aspect of genetic selection acting on phenotypes, the other aspects being reproductive rate and chance. Although recognizing that chance plays a role, especially in small populations (Fisher, 1922; Wright, 1931), genetic models often explore the advantage of one allele over another. While population dynamicists are usually concerned with population growth, and pay more attention to the survival of females, genes are normally passed to posterity about equally through the sexes. Variance among males, however, is often far greater than that among females (Trivers, 1985). Selection thus operates either totally, when an individual dies before it breeds, or partly, when an individual of either sex fails to achieve its reproductive potential. When a male fertilizes a female's eggs he places his genes 'in trust' to his mate, who often fails or only partly succeeds to oviposit. Naturally, he is selected to endeavour to mate with several females, both to maximize his RS and to spread risk (Section **9.7**). Female insects too are often promiscuous, increasing the genetic variability of the offspring and often enhancing AF (Section **10.2.5.1**). Within a species, size and survival are often related, with large individuals surviving longer, as in dragonflies (Sokolovska *et al*., 2000).

Mortality occurs at three phases of the insect's life. There is *juvenile* (= *developmental*) *mortality*, occurring from egg to emerged adult and, as we saw above, is often huge in populations. Then there is *pre-reproductive mortality* of adults, in particular that of females during maturation, migration, finding mates, or searching for their first oviposition site. Thus, the tachinid fly *Cyzenis albicans* takes ~1 month to mature its eggs (Hassell, 1969), during which mortality occurs. Finally, there is the *mortality of females during oviposition*, which is of general occurrence and reduces AF (Harcourt, 1969; Dempster, 1983; Leather, 1988; Jervis *et al*., 2008). Post-reproductive mortality has little effect on population dynamics, although a few beetles such as *Apion* (Section **6.2.1.2(a)**) linger in this strange phase. Some *Chrysomela* spp. such as *C. crotchi*, a pest of aspen in Canada, may survive winter and oviposit in 2 years, as do some carabid (Murdoch, 1966a; Van Dijk, 1994) and dytiscid beetles. Termite queens are long lived (>15 years). But this phenology is unusual and contrasts with the brief life of adult mayflies, limoniine crane flies and gall midges that often survive less than a day.

Diapause confers greater resistance to a harsh physical factor. It normally occurs at *one specific instar* within a species, but *across* species it may be at any instar (see Table 4.1 in Andrewartha and Birch, 1954; Danks, 2007). A few species diapause in two stages, as in the carabid genus *Calathus* (den Boer, 1968) and in several Arctic insects. Here and in cool higher latitudes, diapause is often induced by reducing photoperiod if temperatures are below a threshold (Danks, 2007), and adapted for winter survival. These factors again interact in the maintenance and termination of diapause (Tauber and Tauber, 1981). In the tropics, diapause often permits survival during the dry season and may be induced by low humidity, high temperature and/or shortage of food.

Diapause and emigration are alternative responses to untenable environmental situations; either insects go into a resistant stage *in situ*, or move away (Southwood, 1977, 1988). Adults, generally having greater mobility than juveniles, should opt for emigration. Such behavioural and physiological responses are at the interface of environment and individual. But both responses occur sequentially, thus several groups of beetles fly and caterpillars often walk to less harsh overwintering sites before entering diapause. Appropriate behavioural reactions are essential in selecting sites for hibernation and aestivation (Leather *et al*., 1993). There is often a negative phototaxis, followed by attraction to dark objects and moist microenvironments. Sometimes thigmotaxis is involved. Comparing the alternative adult strategies of diapause and migration, in both cases individuals have large fat bodies and immature gonads (Rankin and Burchsted, 1992).

10.2.3.2 Survival: Physical factors: General

The experimental estimation of survival in relation to harsh *physical factors* gives a population statistic. It requires that a representative sample of a given instar from a population be exposed to varying levels of a harsh regime, one outside the favourable range (Section **10.1**). For statistical reasons a large sample must be used because one is estimating a proportion (Bailey, 1994). For ecology the regime used should resemble those encountered under severe field conditions. Combinations killing 50% of the population are informative (below). In nature, temperature and moisture distribution are linked inextricably (Willmer, 1982; Zachariassen, 1991). We examine here the mainly inimical aspects of these hygrothermal factors on survival, recalling that their influence on growth within the favourable range has been considered in Section **10.2.2.2**. We are concerned with extremes of temperature, dryness and wetness outside this range, with violent mechanical factors and with environmental chemicals. While the effects of *biotic factors* on survival often depend on the physical environment, they are naturally more complex and will be considered later.

Extremes of temperature and humidity, and in combination the drying power of the air, cause physiological stress to insects and, ultimately, their death. Light is rarely harmful directly, at least to those that live in illuminated conditions (Vandel, 1965). These factors have both intensity and duration. Thus, for low temperature, −10°C intensity and 12 hour duration could approximate to the conditions that overwintering moth pupae in cocoons in the bark of a tree could be exposed to on a cold night in a temperate winter. But a higher intensity of such a factor for a shorter duration might kill as many pupae as a lesser one of longer duration. This leads us to consider such combined effects as a 'dose' of a potentially lethal factor. These may be analysed by the well-known 'dosage' or 'sigmoid' response curve (Finney, 1947) used in pharmacology. A parallel exists between the dose of an inimical physical factor and that of a given insecticide. The *dosage–response curve* expresses per cent mortality as a function of the severity of such a factor (Fig. 10.14). Killing 50% of the sample is the LD_{50} (LD = lethal dose), killing 95% is LD_{95}, and so on. If we compare the cold hardiness of two species at the same site, or of different populations from different sites, we normally use the LD_{50}. But if we compare the effect of two different insecticides on a given species we would use the LD_{95} or LD_{99}, since killing power rather than mean survival is relevant. In relation to a dose of low temperature, the expressions $LTemp_{50}$, specifying the low temperature to kill 50% of the sample, and $LTime_{50}$, similarly for the time, may be used (Howling *et al*., 1994; van Lenteren *et al*., 2006).

The variation of individual abilities in a given population to resist low temperature and humidities is a result of selection in heterogeneous

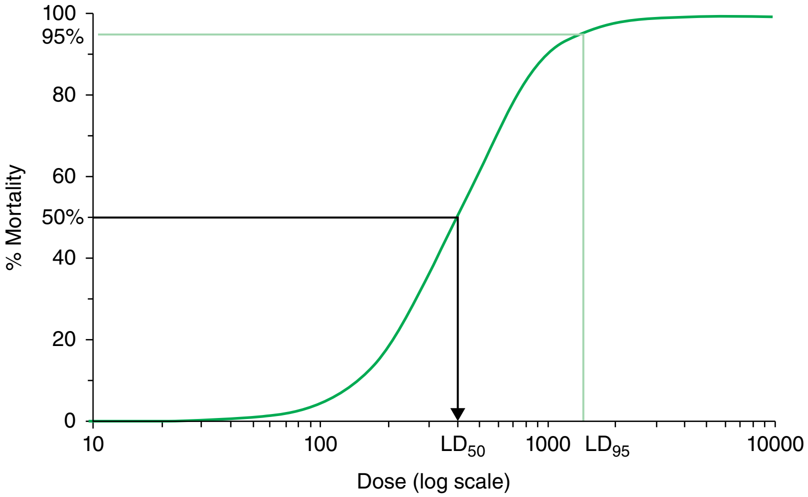


Fig. 10.14. A dosage–response curve. Note the relationship of LD_{50} and LD_{95}.

environments, the *selective mosaic* (Gordon *et al*., 2015; Section **9.1**), especially at the habitat level. Parents produce offspring that vary genetically in these and other traits. Diverse environments and population sub-division (Sugg *et al*., 1996) promote genetic diversity, which is then passed on by parents with enhancing effects to progenies (Ford, 1975). But there are often limits to such evolution (Sections **9.1** and **11.2.3**).

10.2.3.3 Survival: Physical factors: Temperature

Firstly, different temperatures *within* the favourable range (Section **10.1**) have effects on survival. Longevity is commonly less at favourable high temperatures than at favourable low ones. *Thrips imaginis* adults live a mean ~250 days at 8°C but only ~46 days at 23°C (Andrewartha and Birch, 1954). In two braconid parasitoids of aphids, *Praon palitans* and *Tryoxys utilis*, adult females live a mean of 20 and 14 days at 18°C but only 9 and 8 days at 27°C, respectively (Force and Messenger, 1964). Female *Meteorus trachynotus* (Braconidae) live ~45 days at 12°C but only ~10 days at 30°C (Thireau and Regniere, 1995). Adult *Rhagoletis pomonella* live longer at lower temperatures (Boller and Prokopy, 1976). For laboratory *Therioaphis maculata* populations, mean longevity is 99 days at 10.5°C but only 33 days at 29.4°C (Messenger, 1964b), although survival to maturity was 100% between these limits. This effect is, of course, an outcome of faster growth, maturation and senescence at high temperatures.

Long periods of cold, when insects are in chill coma, also increase mortality (Mellanby, 1939; Johnson, 1940; Bale, 2002; Denlinger and Lee, 2010). But the effects of low temperature during the season when juvenile insects are *not in diapause* are especially under studied (Lyytinen *et al*., 2009). At both ends of the favourable range, very low or excessively high temperatures act directly as mortality factors, or engender death or malformation at a later stage. In winters at high latitudes, subzero temperatures can kill insects by causing the growth of ice crystals which physically damage their tissues. Most species combat this danger by seeking insulated refuges (Section **9.9**; below) and entering diapause, converting their glycogen stores into cryoprotectants (Storey, 1990). There are two diapause strategies: *freezing intolerance* (= freeze avoiding) and *freezing tolerance* (Bale, 2002; Denlinger and Lee, 2010). Both may employ similar cryoprotectants such as ice-nucleating agents (INAs), antifreeze proteins (AFPs), polyhydroxyl alcohols (polyols) and sugars. In the former strategy, the adapted instar increases its fat content, clears its gut of food, loses water, masks or eliminates nucleation sites (including bacteria) where ice starts to form, and converts much of its glycogen into protectants. Apart from glycerol, polyols include sorbitol, ribitol, threitol and erythritol (Storey, 1990). Shock proteins, which assist protein transport under severe conditions (Relina and Gulevsky, 2003), may also be synthesized. As temperatures fall a little extracellular ice may form in isolated tissues but this is unlikely to be fatal. But at a critical low temperature, which varies with species and individual, the '*supercooling point*' (SCP), a sudden, lethal wave of freezing sweeps through the body. SCPs are often used in physiological studies of insect cold hardiness (see Table 2.1 in Lee, 1991). But they may not be a good proxy for effective cold hardiness in the field (Hiiesaar *et al*., 2009). We might expect normal statistical variation in SCPs, but in the weevil *Ceutorhynchus obstrictus* (Cárcamo *et al*., 2009) a marked skew exists. Most SCPs lay between −4.5°C and −8.5°C, but there was a long tail reaching to −18°C, a few adults being very cold hardy.

We noted above that bacteria could act as INAs. But different bacteria reduce the super cooling point of *Cacopsylla* by different degrees (Lee *et al*., 1999). Thus, *Pseudomonas putida* has a far greater effect than *P. syringae*. The authors suggest the principle might be used in pest control. Spraying water on these diapausing bugs also marginally reduces their survival in cold weather, an effect that may well occur in nature when a rainy day is followed by a clear, frosty night.

By contrast, *freezing-tolerant* insects can withstand freezing itself (Salt, 1961; Lee, 1991; Duman, 2001; Bale, 2002), although this is confined largely to extracellular areas. Such insects are often found in very cold regions and habitats (Turnock and Fields, 2005). Thus, in the UK the wood-boring larvae of *Tipula selene* are tolerant of such freezing (when frozen you can snap them like twigs!) and generally survive temperatures as low as −12°C (Freeman, 1967b). In some extremely freezing-tolerant insects, water does not freeze in damaging crystals, but through the action of cryoprotectants (Duman, 2001), forming a homogeneous 'glass' that inhibits all molecular diffusion. Danks (2007, see Table 3) lists many adaptations of insects to low temperatures.

The degree of cold hardiness that some insects achieve is considerable, and as we saw has been selected for by the severity of winters their ancestors have survived. In the Northern Hemisphere, northerly populations have greater hardiness than southerly ones (Fig. 10.15). In central Canada, where winter air temperatures may fall below –40°C, such insects convert considerable metabolic resources to synthesize polyol antifreeze (Danks, 1978). An amazing 25% of the mass of larval *Bracon cephi* (Section **4.4.1.1(b)**) may be glycerol, and its SCP ~ –47°C. The more antifreeze in such insects the greater their ability to survive, but the more metabolic resources they commit. This polyol also allows rapid cold hardening (Lee *et al*., 1987). So, in far northern populations we might expect a trade-off, females retain less of these resources to build the ovaries and hence their MPF would diminish. But polyols can be interconverted with glycogen, a store available for later reproduction (Storey, 1990). The interaction between survival and fecundity, relating to Fisher's Fork (Section **9.7**), requires qualification. Similar re-use of defensive metabolites and cryoprotectants for other purposes occurs in plants (Section **2.4.2**). But in insects the time at which feeding stops is critical. Food in the gut is a focus of freezing, so larvae must clear it in autumn and diapause early to avoid the *risk* of a sudden cold spell (caught with their guts full!). They trade survival for growth. In some bivoltine moths, such as *Cydia pomonella* and *Plutella xylostella*, the overwintered generation indeed has lower AF than that of the summer one (Leather *et al*., 1993), so we might expect The Fork, but in such cases potential effects of food quality must be understood.

Diapause is induced by various factors, but reducing photoperiod (Beck, 1980) and temperature in early autumn are critical, as in *Aedes taeniorhynchus*. Pre-conditioning with low temperature (*acclimation* or *cold hardening*) for just a few hours can enhance cold hardiness (Mellanby, 1939), promoting rapid protection when sudden cold weather approaches (Lee *et al*., 1987; Coulson and Bale, 1990). Cold adaptation is dynamic not static, adjustments and even repairs are made during winter in response to extant conditions (Danks, 2007). Naturally, there may be repeated bouts of freezing and thawing with diverse effects on cold hardiness. It is also critical that individuals do not come out of diapause in a mild winter, only to die in a cold spring, and adjustments must be made to achieve this. Laboratory *Myzus persicae* populations can tolerate simulated nightly frosts down to –5°C for several days, but acclimation is critical (Howling *et al*., 1994). But what effects ensue after *surviving* low temperature? Again, we separate individual from population processes (Section **9.6**). Individuals may suffer reduced survival or diminished AF *manifest after winter*, as in *Diuraphis*

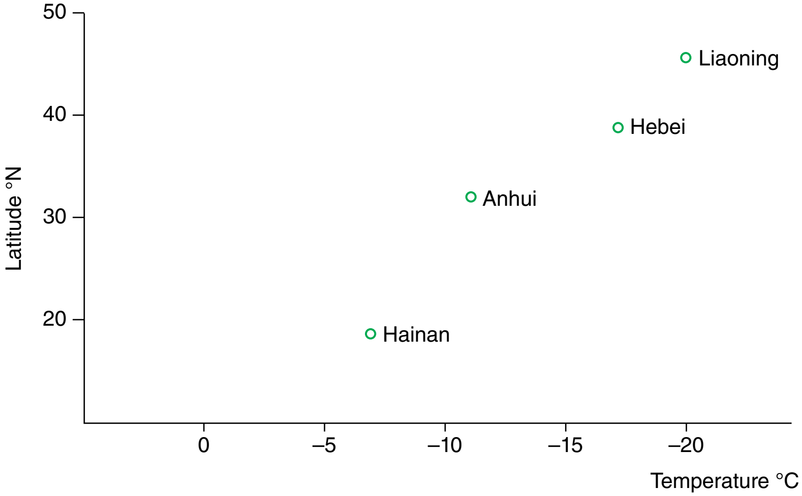


Fig. 10.15. The effect of a latitudinal gradient on cold hardiness in *Locusta* eggs. Data from Jing and Kang (2003) *Ecological Entomology* 28, p. 151. Reproduced with permission.

noxia (Butts and Schaalje, 1997). Then, when extreme cold selects for very cold-hardy individuals, they may have attributes, for example, AF, that are different from the mean in the starting population. Some bad effects may be caused by damage to intracellular symbionts (Parish and Bale, 1991). Such bacteria are usually transmitted vertically via the eggs (below), and their own defences against winter cold would make an informative study.

Recall that behavioural as well as physiological strategies are used to combat harsh conditions (Southwood, 1977; Duman, 2001; Denlinger and Lee, 2010). Winter stages often seek less cold microenvironments prior to winter, as in clover seed weevils (Section **6.2.1.2(a)**) and related beetles, and in the bug *Javesella pellucida* in Finland. But both *less cold* and *very cold* places may constitute *thermal refuges*. Insects in the soil often move down from the cold surface layers. But the physical severity that a focal species can endure can be *its defence against the biotic* one that enemies might impose. Thus, larvae of the hover fly *Syrphus ribesii* remain in the coldest, superficial region of leaf litter and are extremely freezing tolerant (Hart and Bale, 1997), a strategy probably reducing predation. The diapausing eggs of many aphids and moths survive on twigs and branches where only specialized, avian predators such as titmice can reach them (Betts, 1955). The eggs of northern populations of *Epirrita* (Geometridae) can withstand –36°C, while those of some aphid species tolerate –30°C for a month (Strathdee *et al*., 1995). Eggs of *Pemphigus betae* in Canada resist –40°C (Harper, 1963). Some aphid eggs contain mannitol and glycerol and are black, making them less visible when concealed in crevices.

Within a locality, say 1 km^2, species living in exposed places usually have greater hardiness than those from more protected ones. This difference occurs in related species living together, as in a study on larval *Tipula* spp. (Freeman, 1967b), collected directly from the New Forest. Experimental regimes were 10 hours at –5°C and –10°C, similar to those often found there on a cold winter's night. LD_{50} values could not be used, as several species were uncommon. Semi-aquatic species (*T. maxima*, *T. fulvipennis*), that live where water buffers them from low extremes, were all killed by a –5°C exposure. *Tipula paludosa* from damp pasture had 62% mortality at this regime. *Tipula marmorata* and *T. irrorata* from mosses growing on fallen logs all survived –5°C. *Tipula selene*, which mine small fallen branches, had the greatest cold hardiness. Of 65 larvae tested, none were killed by –10°C, at which no other species survived. Similarly, in ladybirds, those that hibernate under snow generally have less cold hardiness than those that do so above it, for example, in chinks in bark (Coyle *et al*., 2011; Hodek, 2012). It can be hard to prove that physical factors have killed insects in the field (Richards, 1961), but with crane fly larvae dying from cold the effects are diagnostic. After severe frost they can be recovered either still frozen solid or flaccid. Dissection when thawed reveals the lacerations caused by ice crystals. More generally, the heterogeneity of low temperatures experienced at diverse spatial levels (Levin, 1992) provides *islands of favourability* (i.e. refuges; Section **9.9**) where many insect species overwinter successfully.

The cold hardiness of such larvae in England is far exceeded by those living in the extreme cold of inland Canada. Large larvae of the mountain pine beetle have an LD_{50} of –34°C (Section **4.2.1.2(h)**), the oak borer, *Synchroa*, can survive –40°C, while *Cephus cinctus* in wheat stalks (Section **4.4.1.1(b)**), have an LD_{50} of 28 days at –20°C. In Poland, *Lymantria monacha* larvae resist –40°C (Szujecki, 1987). In Norway, eggs of the larch budmoth (Section **5.2.1.4(d)**) survive –50°C. Although larvae of the Arctic moth *Gynaephora groenlandica* freeze at –8°C they are able to survive –70°C (Strathdee and Bale, 1998).

Overwintering Colorado beetles in Canada, however, have an LD_{50} of only –7°C for an overnight exposure, similar to that for *T. paludosa* in England. Precise data from New Brunswick (Boiteau and Coleman, 1996) give an LD_{50} of –10°C for a 3 hour exposure. Adults that have not found more protected places (Hunt and Tan, 2000) burrow into the ground before winter and, because of the natural insulation provided by soil, the lower they go the greater protection they obtain. Data from Saskatoon (52°N) under turf show that an air temperature of –40°C would be associated with soil temperatures of roughly –10°C at 10 cm and –5°C at 50 cm. Such temperatures could be rather lower if a period of very cold weather persisted. The depth the beetles penetrate depends on the friability of the soil and type of cultivation used. Because potatoes thrive on deep cultivation, long (~60 cm) tines are often used to break up the subsoil prior to ploughing. If they are not, a hard pan forms below the depth to which the ploughshare penetrates, commonly <30 cm. This pan restricts the downward movement of the beetles. In harsh winters in northern North America, when the air temperature might be < –20°C, a considerable proportion of them freeze to death. So there is a link between the type of cultivation and the survival of the beetles (Section **13.2.3.5**). Snow also provides insulation in direct relation to its depth. So, the high risk of low winter temperature in higher latitudes is a factor limiting the northward spread of these beetles. Similar reasoning applies to pests such as cutworms, wireworms and cockchafer grubs (Section **3.2.1.2**) overwintering in the soil in cold climates. But while greater depth provides greater protection, deep soil warms up more slowly in spring causing the emergence of insects there to be later, hence wasting time (Danks, 2002).

By contrast, some species from warm countries die just above 0°C, an effect caused by membrane damage, and called 'chilling injury'. *Cimex* eggs (Section **7.3.1.2**) have an LD_{50} of ~12 days at 2°C, rising to ~20 days at 4°C (Johnson, 1940). Tropical stored-products beetles (*Lasioderma serricorne*, *Calandra oryzae*; Section **6.3.1.2**) and eggs of *Locusta migratoria* are soon killed at ~5°C, as are tropical fruit flies (Section **6.3.1.2**). *Tricoplusia ni* pupae at Vancouver suffer death or deformity after long exposures of only 10°C (Caron and Myers, 2008). Temperatures near zero may limit the spread of *Eccritotarsus catarinensis*, a bug used to control water hyacinth in South Africa (Section **8.2.3**). These facts may explain why most tropical pests do not penetrate temperate regions, or if they do so are confined to protected conditions in buildings, silos and like structures. Thus, adult *Culex pipiens* overwinter in great numbers in New York City sewers. In London, *Periplaneta americana* cockroaches are often found in hospital basements. I have seen them. These beasts are a common nuisance in abattoirs. In north temperate regions, such as Canada and Sweden, temperatures near zero can occur even in June. In larval *Neodiprion sertifer*, such summer temperatures cause significant mortality (Olofsson, 1986). Eggs of the nymphalid butterfly *Polygonia c-album* are killed by such temperatures (South, 1906).

High temperature inactivates enzymes, progressively breaks down structural proteins, disrupts membranes and allows build-up of catabolic products inducing metabolic collapse (Willmer, 1982). Discounting endothermic and specialized species (see below and Section **10.2.4.2**), insects do not combat this so much by specialized *physiology*, as they do with low temperature, but *behaviourally* by moving to cooler microclimates should they exist. Insects are hyperactive and show escape reactions as they start to get too warm. Small foraging bees under extreme insolation within flowers overheat and apparently take short flights to cool down (Corbet and Huang, 2016). Even so, several groups such as locusts, sand wasps and velvet ants are adapted to hot places. In the tropics, the wasps *Sphex* and *Bembix* dig their burrows in sand when under extreme insolation and surface temperatures exceed 50°C. They pass rapidly through hot surfaces into the cooler sand beneath, a behaviour adapted to microtopography and recalling the link between intensity and duration of an inimical factor. The LD_{50} values of South African blow fly larvae are high in relation to the extreme temperatures (max. 49.3°C) in the carcasses they infest (Richards *et al*., 2009). Of seven species, *Calliphora croceipalpis* has the lowest LD_{50} (42.9°C) and *Chrysomya marginalis* the highest (50.1°C). The authors suggest that the heat generated by great masses of maggots is involved in determining the course of interspecific competition on big carcasses.

But the inimical effects of high temperature may be delayed. In *Anastrepha* (Section **6.3.1.1**(**l**)), larvae exposed to ~40°C may survive temporally, only to die during pupation (Andrewartha and Birch, 1954). The adults of species from hot, arid regions, such as some dacine flies and red locusts, enter diapause during drought and have enhanced resistance to such extremes. High temperature may affect endosymbionts before it affects their insect hosts. In aphids, *Buchneria* die long before their hosts, although other such bacteria like *Serratia* and *Hamiltonella* (Section **5.3.1.2**(**h**)) reduce this effect (Harmon *et al*., 2009, in Feldhaar, 2011).

10.2.3.4 Survival: Physical factors: Precipitation and moisture

Water in its various states, in combination with other physical factors, affects insect survival directly, or indirectly (Dempster and McLean, 1998), driving biotic ones such as food and enemies in a causal chain (Sections **10.1** and **12.3.4.3**). Extreme dryness or wetness can be *directly* lethal to individuals, so reducing the survival of populations. Low humidity is ultimately the result of a lack of precipitation, especially rainfall. *Drying power of the air* is a good measure of field aridity (Section **10.1.1**), where low atmospheric moisture, high temperature and wind speed act together. Because insects are small they have a high ratio of body surface to body volume (**1.2.**) and are *potentially* prone to lose water rapidly by evaporation. When they desiccate directly, the ionic concentration of their haemolymph and other tissues rises, finally causing metabolic collapse. But they have evolved several effective means of *avoiding* and/or *combating* desiccation, which we will consider together.

An insect's *water balance* has negative and positive components (Edney, 1977). Water evaporates from the integument, is lost via the spiracles during respiration, and with excretion and defecation. Waterproofing, however, has its limits. Because the oxygen molecule is larger than the water molecule (about 50% wider), no insect or other animal (Hinton, 1969) has been able to evolve a membrane that is at once impermeable to water but permeable to oxygen. So water conservation and respiration are at variance. This fact is critical for immobile stages (eggs, pupae) that cannot seek free water. Insects reduce water losses by *behavioural and physiological mechanisms* (Wigglesworth, 1984). Stressed insects seek less arid locations, and may attempt to obtain free water (below). Bees and cockroaches stem integumentary water loss by a hormonal mechanism. Surface waxes reduce such losses and give various levels of impermeability. Depending on species, the efficiency of the wax breaks down at a critical temperature. In larval *Nematus* and *Pieris* (Sections **5.2.1.3** and **5.2.1.4**), this occurs just above 30°C, not an inordinately high field temperature, especially during insolation. But in many insects the waxes resist higher temperatures. The amount of water that insects lose during respiration, which can be high in tetrapods, is low when insects rest, as their MR is much reduced, often to only one hundredth of that while flying. Tsetse (Section **7.3.2.4(m)**) searching for blood meals, but resting periodically, provide an example. Many insects survive proportionally greater tissue desiccation than most birds and mammals. The big woodland crane fly, *Tipula fulvipennis*, can lose 25% of its body mass and, like a camel, regain it by drinking (Freeman, 1968). Some desert insects tolerate an even greater level of desiccation (Edney, 1977). Insects in diapause, however, may desiccate gradually, even during temperate winter (Zachariassen, 1991), as they are inactive and cannot replace evaporative losses. But their respiratory needs are very low.

Fluid water is gained by seeking and drinking it and with the food. Adults usually find free water quickly and, because of their small size, minute amounts such as dew drops can rehydrate them. Others absorb it through the integument, as in *Cephus cinctus* (Section **4.4.1.1(b)**). In arid habitats, insects such as *Xenopsylla cheopis* (Section **7.2.2.2(a)**) absorb water vapour at relative humidities <50%. Water is also produced internally as a metabolic by-product. Adaptations to extreme aridity, like those to extreme cold, often show dynamic metabolic adjustment, especially in relation to the state of internal water (Danks, 2007).

As with low temperature, the mortality of insects due to dry air, or simply their rate of weight (~water) loss, may be assessed in the laboratory on samples of a population and the results analysed by the dosage–response curve (Section **10.2.3.2**). Naturally, they are not fed under experiment. As expected, the ability of an insect to resist desiccation is commonly related to the drying power of its normal environment (Edney, 1980). *Anastrepha* pupae in the soil die if it is either too dry or too wet (Aluja, 1994). But investigation of desiccation rates may reveal new insights into an insect's ecology (Danks, 2007). Thus, the larvae of *Tipula irrorata* and *T. marmorata* live in the UK under mosses on walls and fallen trees (Section **10.2.3.3**). In spring, when both species are in the third larval instar, they have a similar resistance. In the fourth instar in summer resistance of *T. irrorata* remains about the same, but that of *T. marmorata* increases *14-fold* (Freeman, 1967b). This *physiological* difference has a marked effect on their ecology in dry years. In exposed microenvironments *T. marmorata* persist, while desiccated, shrivelled, moribund *T. irrorata* larvae can be found in the same place. If the difference in their drought hardiness were unknown such an outcome might be spuriously referred to as the result of resource competition. But in moist microenvironments both species survive together (**Table 10.4**).

On the other hand, excessive moisture has lethal effects on many species. In those adapted for normally arid environments, such as locusts, wetness may kill them directly from water logging or indirectly from pathogens, especially from fungi (*Aspergillus, Beauveria, Entomophthora*, *Spicaria*) which spread rapidly at high humidities. This interaction between a physical factor, a pathogen and survival is comparable to the one between temperature, *Trialeurodes* and *Encarsia* (Section **10.2.1**). It re-emphasizes that the physical environment sets the rules for the biological games that are played (Huffaker and Rabb, 1984), be they competition, cannibalism or the effect of an enemy or pathogen. In the soil, overwintering pupae of *Heliothis armigera* (Section **6.2.1.2(d)**), *Tyria* (Dempster, 1982), wireworms and many other insects, drown if it becomes saturated for long periods, an event more likely when it is rich in clay and in *a low-lying situation*, the latter being a topographical effect. We see that edaphic factors (Wardle *et al*., 2004) and topography, even microtopography, may be influential. For topography, when *Trypoxylon palliditarse* breeds in deep valleys in Trinidad its nests are smaller and its juvenile mortality greater than in more exposed situations, even when MAP is similar (Freeman, unpublished data). In the Netherlands, more than 95% of larval *Calathus melanocephalus* (Carabidae) drown if winter is very wet (den Boer, 1998). In the New Forest in the UK, the distribution and possibly survival of the larvae of four *Tipula* spp. at the edge of low lying carrs is associated with the chance of flooding in summer and also pH (see Figs 2 and 3 in Freeman, 1967b). Winter flooding here drives *Tipula* larvae to the soil surface where they are vulnerable to night frost, another interaction between physical factors. Larval bark beetles die in their tunnels from drowning and larval *Asphondylia* midges die in their galls during long periods of rain (Freeman and Geoghagen, 1989). For microtopography, Courtney and Duggan (1983) record frequent cases of drowning in *Anthocharis* caterpillars (Section **9.1**), particularly when they feed on waterside crucifers. Insect eggs that survive in difficult conditions for respiration are often equipped with a *plastron,* a type of gill possessing an extensive water/air interface (Hinton, 1969). Apart from aquatic situations they are found in species in several orders in which eggs are subject to repeated wetting and drying. In some cases wetting can reduce respiration, increase development time, and so lead to an Allee effect (Section **10.2.2.4**).

Populations of spruce budmoths (Section **5.2.1.4(c)**) and some cutworms are sparse in wet years. *Glossina tachinoides* (Section **7.3.2.4(n)**) fails to feed in wet conditions and this increases its death rate. Heavy rainfall also has mechanical effects (Section **10.2.3.6),** while small insects are often caught in films of water and cannot escape (Section **2.1**). For endophytic herbivores especially, moisture may act indirectly via the plant. In the stem-galling sawfly *Euura lasiolepis*, juvenile survival is less under experimental drought (see Table 13.9 in Price, P.W., 1997). In a complex interaction, oviposition in the sawfly *Neodiprion* itself leads to the desiccation of pine needles and in train to that of the eggs (Codella and Raffa, 2002; Section **5.2.1.3(b)**). Conversely, moisture reduces the survival of juvenile *Trypoxylon palliditarse*, as it promotes the success of their enemies, possibly because the latter penetrate its mud cells more easily when these are damp (Freeman, 1981a).

10.2.3.5 Survival: Physical factors: Light

In Section **10.1.1** we distinguished *incident light* from *reflected light*. The latter is essentially a modification of the former due to selective absorption by natural objects, either living or dead. Both forms of light diversely affect survival. Without light the various colours and patterns insects and plants possess would be meaningless: they function only in daylight (Rothschild, 1972). But the *light environment* in which they are seen alters perception. In the past, our senses were spuriously viewed as flawed (Section **11.5.1**). Endler (1992) classifies habitats according to the light regimes they possess.

First, we consider the effects of *incident light*. Insects use both diurnal and annual changes in their variation as cues to ascertain the time of day or season of the year, namely '*temporal orientation*', so providing essential information for survival. In general, they are adapted for activity either by day or by night. Houseflies, however, may be annoyingly active during the day and in illuminated rooms at night. But normally, either in the fading light of evening or in the increasing light of dawn, insects seek refuges in which to pass their resting periods. Of course, great differences exist in the photoperiodic regime, both diurnal and annual, between tropical and high temperate regions, there being much greater variation in the latter. Insects everywhere are adapted to such regimes. Photoperiod provides a reliable clock and cue for temperate insects to determine their position in the annual cycle and when to enter diapause (Danks, 2007). Reducing day length, irrespective of temperature, induces diapause in *Bombyx mori* eggs, *Grapholitha molesta* larvae and *Diataraxia oleracea* pupae (Section **10.2.3.1**). Without such diapause induction they could not survive winter (Section **10.2.3.3**). But photoperiod often acts with temperature (see Table 2 in Mousseau and Dingle, 1991). The larvae of some *Aedes* and *Anopheles* (Anderson, 1968) and many adult beetles enter diapause using this combination. In *Lucilia,* the inception of diapause within the puparium is unaffected by light, possibly because many are in dark places and/or because light cannot penetrate the puparial wall. But in another blow fly, *Calliphora vicina*, maternal effects induced by day length, supervene (Vinogradova, 1974). Several insects also use incident light for *spatial orientation*, in turn influencing survival. Others, including locusts and honey bees, use the pattern of polarized light for orientation (Section **10.2.4.4**).

Second, insects use colour, pattern and intensity of *reflected light*, to seek resources (Section **10.2.4.7**) and avoid enemies, both affecting survival. Nocturnal and cavernicolous predators find their prey by tactile and chemosensory clues. Cave insects are generally blind and depigmented (Vandel, 1965). By contrast, nocturnal insects have functional eyes and are variously pigmented since they must stay hidden and avoid predation during the light of day. Herbivores such as aphids respond to the exact spectra of greens and yellows coming from specific food plants. The butterflies *Papilio andraemon* and *P. demolius*, the weevil *Exophthalmus vittatus* and the leaf miner *Phyllocnistis citrella*, are all attracted to the light green flushes of young citrus leaves, again affecting survival. Their predilection for yellows results from a bias in their sensory processing (Kelber, 2001), a bias allowing us to trap them to investigate and perhaps to control them (Section **13.2.3.5**(**d**)).

Much attention has been paid to strategies insects employ to avoid being eaten by visually hunting predators, especially tetrapods (Cott, 1940). These ploys variously reduce the efficiency of such enemies (Section **10.2.3.9**). Insects seek refuges where they are not seen easily, assume atypical postures and/or use various types of coloration; they avoid detection relative to the perceptual abilities of their predators (Sections **5.2.1.3**(**b**) and **8.2.1.1**). Colour and pattern may blend with the background, look like ubiquitous objects (*crypsis*) or resemble other animals (*mimicry*). All are types of natural deception (Section **10.1**). I regard disruptive patterning as a form of crypsis as it functions against specific backgrounds. Some insects, however, contrast with the background, advertising their true nature. This may be for (i) mate recognition or (ii) to advertise their harmful properties to potential predators (*aposematism*). The Lepidoptera especially employ the coloured scales on their wings diversely in ways that do not impair flight. Indeed, insect coloration in general is relative to habitat, and mainly to its light environment (Endler, 1992). The wings of woodland crane flies (*Tipula fulvipennis*, *Limonia nubeculosa*) are dappled and cryptic, those in open habitats (*T. lateralis*, *T. paludosa*) are plain or striped lengthwise. So, insect colour patterns have diverse behavioural and ecological outcomes. Behaviour maximizes their effectiveness, but ecologically they may limit distribution at the habitat level.

Many cryptic folivores (some hawk moth larvae, katydids) closely match the leaves they feed on. Others (some geometrid larvae) resemble dead twigs. Resting adult *Polygonia c-album* (Nymphalidae) look like dead leaves. Such objects are ubiquitous in nature, which improves hiding (Hinton, 1973; Schaefer and Ruxton, 2009). They are unlike a predator's search images (Vane-Wright, 1980), so their signal-to-noise ratio is less. There is also a premium on randomness. In crypsis and mimicry, the ratio of density of the deceiving insect relative to that of the object resembled is important for success. There is density dependence. Deceiving insects should be *relatively* rare. Following this, crypsis is often combined with polymorphism (Turner, 1987), so reducing effective density. *Xylophanes chiron* (Sphingidae) has green or brown adults, while the tortrix *Acleris variana* (Miller, 1966) and *Achaea lienardi* (Noctuidae) have many forewing patterns. The British moths *Procus strigilis*, *P. furuncula* and *Apamea secalis*, and the Australian bogong moth *Agrotis infusa* (Noctuidae) are similarly patterned. Great colour variation exists in *Acrydium arenosum* (Tettigidae). In the abundant Caribbean grasshopper *Orphulella punctate,* there are green, green and brown, and brown morphs, combined with four patterns (plain, mottled, striped, zebra) (Dixon, 2008). Such complexity attests to the selective pressures exerted by avian predators. Cryptic morphs are usually female, those disruptively patterned (striped, zebra) usually male. Crypsis is sex linked. Final instar larvae of *Eurytides marcellinus* (Papilionidae) have blue-green, brown, and black morphs (Garraway *et al*., 1993b). Thus, if a predator learnt to crack such crypses quickly (Trivers, 2002, p. 9), it would perceive its polymorphic prey falsely to be a set of different foods, tending to make searching longer (Allen, 1988; Bond, 2007). Also, multiple showy patterns tend to be avoided by naïve predators, called *neophobia* (Mallet and Joron, 1999; Gordon *et al*., 2015; Section **3.2.2.1**(**b**)).

But the pattern of the background against which morphs are seen, their light environment, varies. In aquaria, green morphs of the bug *Sigara* are better protected from predation by fishes on green surfaces than on brown ones and vice versa for brown morphs (Popham, 1942). In the field, experiments on melanic forms of the moth *Biston betularia* in natural and industrial environments (Kettlewell, 1973) show the considerable value of background matching. Backgrounds themselves can assist crypsis, highly variable ones tending to conceal potential prey, especially if the prey are highly variable, as are the moths *Acleris* and *Achaea* (Merilaita, 2003; Bond, 2007). Namely, certain intimate backgrounds offer safer resting places than others, which, if selected by a species, could be regarded as resources (Section **9.8**). So, the multiplicity of forms shown by such insects may serve to reduce predation from tetrapods. It certainly makes them less visible to human eyes on a variety of backgrounds. Hinton (1973) asserts that what can fool the professional entomologist will certainly fool an avian predator, although one appreciates that our spectral sensitivity has differences from birds, who can see into the ultraviolet (Ratcliffe and Nydam, 2008). But work on several species by E.B. Ford and his students, by M.D. Bowers (Brower, 1984), and by H.E. Hinton himself supports his view.

Insects such as larval spurge hawk moths *Celerio* (= *Hyles*) *euphorbiae* are brightly coloured, truly advertising their poisonous nature. This is *not deception*. Their brightness and appropriate behaviour allows predators to identify them at distance, so avoiding close-up mistakes (Endler, 1992). Such insects either produce their own toxins, as do ants and wasps, or obtain them from plants (Hinton, 1973). The colourful larvae of danaid butterflies sequester poisons from asclepiad food plants. Conspicuous black and yellow cinnabar caterpillars obtain poisonous alkaloids from ragwort (*Senecio*; Section **10.2.3.8**). The adults, however, are black and red and synthesize histamine. Some but not all poisonous butterflies (Vane-Wright, personal communication) have females with slower flight and larger abdomens and ovaries than cryptic females. Aposematic colours may give less predation and greater AF (Marden, 2000). But protective or deceptive coloration in adults may compromise conspecific sexual signals, as in *Papilio dardanus* (Cook *et al*., 1994). So natural selection for survival may differ from sexual selection (Andersson, 1994; Sections **9.1** and **10.2.5.1**). In male tiger moths, *Parasemia plantaginis*, mating success in both white and yellow morphs is greater which ever morph is in the majority, but survival depends on the species of avian predator (Gordon *et al*., 2015), a selective mosaic exists (Sections **9.1** and **9.7**).

But what is cryptic at one spatial scale can be warning coloration at another. When massed cinnabar larvae on a yellow ragwort flower head are seen from a distance the effect is cryptic, but warning when a single larva is examined close up (Dempster, 1982). A similar effect may well apply to mullein shark larvae on the yellow floral spikes of their food plant. Indeed, distance is often a factor in defensive behaviour, largely in relation to the visual acuity of a potential predator. Yellow underwing moths, *Noctua pronuba*, and peacock butterflies (below) employ passive crypsis at a distance but active, *startle behaviour* close up. In this butterfly experiments show the mechanism's great effectiveness when avian predators are near (Vallin *et al*., 2005). In defensive behaviour, most social wasps and bees are actively aggressive towards a potential enemy only when they are close to their nests. Then, stingless male *Polistes crinitus* wasps have the same coloration as females (*automimicry*) and mimic their stinging behaviour (Freeman, unpublished data). Boppré *et al*. (2017) suggest that many wasp species share a common black and yellow pattern to avoid mutual aggression.

To continue, there are many other cases of the multiple functioning of insect pattern (Hinton, 1973; Rothschild, 1984; Trivers, 1985), and the term *dual signalling* has been applied, although *multiple signalling* is often more fitting. Cryptic form may change during a larva's life apparently to accommodate the fact that it is getting bigger. Young larvae of *Saturnia pavonia* (Saturniidae) are blackish but green and black when mature. Those of *Papilio homerus* resemble lizard's faeces when small, then bird's faeces and finally become cryptic green, but also develop a snake-like 'head' (Garraway *et al*., 2008). A snake's head deception by larvae is also seen in some other Papilios and in the Neotropical moth *Leucorhampha* (Hinton, 1973). Resemblance to a tetrapod face, in total or just the eyes, is common. Resting *Daphnis nerii* (Sphingidae) have green cryptic wings, but an aggressive-looking mammalian face on the thorax (Fig. 10.16), one seen in stages of evolution in congeneric species (D'Abrera, 1986). Such defences are

Fig. 10.16. The hawk moth *Daphnis nerii.* At a distance the green and brown pattern is cryptic, but close inspection reveals a sinister image, construed as warning coloration. Like effects of distance occur in *Cucullia* (Fig. 5.3) and *Tyria* (Section 8.2.3) larvae. Source: Wikimedia Commons, author Sugata Banerji.

helpful in such big moths that need a warm-up period before flight (Heinrich, 1977). Resemblance to a gecko's head appears on the closed wings of the butterfly *Caligo illioneus* (Martin, 2012). The head shape, eye and tympanum are all mimicked in correct placement. Remarkably, the bug *Fulgora lucifera* mimics the head of a small alligator (Hinton, 1973). Similarity to a much larger animal has no evolutionary outcome for that animal, but when another insect of similar size is mimicked there may well be (below). This bug also has big eyespots on its hindwings, which it displays if all else fails. Of course, eyespots are common on butterfly wings, large ones functioning to frighten small birds (Vallin *et al*., 2005; see above), small marginal ones diverting attention to less vulnerable areas (Blest, 1957). Again, such defences work only with appropriate behaviour, not with dead insects. In the Jamaican *Papilio homerus* the upper wing surfaces are yellow and dark brown, which could operate as a startle pattern (Sargent, 1990). But the wide, dark brown wing margins define an inner arena with the colour and markings reminiscent of several common, local skipper butterflies, especially *Epargyreus antaeus* and *Chioides catillus*. Such an image is also visible on the lower wing surface when the forewings are extended, as in take-off. Note that a multiplicity of similar models improves the effectiveness of deception (Mather, 1955).

Hespenheide (1973) reports a case where a group of zygopine weevils and agile Diptera found together on the boles of trees, have like colour patterns. He suggests this deception might work because avian predators have learnt the difficulty of capturing the flies, a vain activity incurring costs. In the *Papilio* case, the skippers resembled are much smaller and have rapid take-off and flight. Experienced birds may avoid chasing them, as in Hespenheide's example, since the chances of capture and the trophic reward would be less. Such deception would act like Batesian mimicry involving a distasteful model (below), but here potential predators would learn to avoid wasting time instead of being poisoned, prey having a lower risk of capture. This possible '*catch-me-if-you-can mimicry*' involves a *deception of scale* for the Lepidoptera, but not for the weevils. Then, several Papilios and some big moths have one or several V-shaped lines across the wings subtending a smaller area or areas, perhaps further cases of deception of scale. Hinton (1973) notes that diffraction gratings on the elytra of some carabid beetles may make it hard for predators to judge distance. Possibly the V-lines of these Papilios function similarly. Note, I mention the above more as conjecture rather than hypothesis.

Anti-predatory devices work better in combination (Gross, 1993), as do size, agility, warning coloration and chemical defence in tiger beetles (Pearson, 1985). Tiger moths employ warning coloration against birds and ultra-sonic clicks against bats (Ratcliffe and Nydam, 2008). 'Using many sensory modes is always better than using a few or one' (Endler, 1992). Also, there are cases of cryptically patterned species being poisonous, as in the moth *Mania typica* (Fisher, 1930), the bug *Nezara* and the larvae of several sawflies (Prop, 1960, in Sillén-Tullberg, 1988). But while crypsis protects them from visually hunting tetrapods it is useless against enemies using olfaction. Larvae of *Battus philenor* (Papilionidae), however, deter the ichneumon *Trogus pennator* by having unique alkaloids in their integument, sequestered from their *Aristolochia* food plants (Sime, 2002).

The verity of such strategies is clear in the colour of lepidopteran pupae. Exposed butterfly pupae use cryptic, mimetic or warning coloration, but those of moths in opaque cocoons or in soil are always brown. For exposed pupae, crypsis may be vital as they are immobile. In a few papilionid butterflies, a green/brown polyphenism occurs. After selecting the pupation site, a brief sensitive period exists, described originally by Poulton (1887), in which brown backgrounds induce a neurosecretory response, causing brown coloration. Against green there is no response, the pupae remaining greenish. In *Papilio polyxenes*, this reduces bird predation (Hazel *et al*., 1998). In dry Californian summers, *Battus philenor* pupae react similarly to substrate colour, but heat also promotes brown colour. This morph often diapauses (Sims and Shapiro, 1983), so there may be an additional adaptation to hot, dry weather. In *Papilio machaon* (South, 1906) and *P. homerus* (Garraway *et al*., 2008), there are green and also brown, variously marked, pupal morphs. But the exposed pupae of *Abraxas grossulariata* (Geometridae) are warningly banded black and yellow (Hinton, 1973) and are distasteful to several birds.

Mimicry, the resemblance of one species to another for protective, aggressive or other purposes, is frequent in insects and has often been investigated in relation to natural selection (Cott, 1940; Sheppard, 1975; Turner, 1987). Plants, too, often employ mimicry (Section **8.2.1**). But for animals, three species or groups, the model, the mimic and the signal receiver, operating as individuals (e.g. a potential predator), are involved. When the model is an insect of similar size, evolutionary outcomes due to mistakes made by the predators ensue. In *Batesian mimicry* the model is distasteful and warningly coloured but the mimic is palatable. As in crypsis, mimicry may involve polymorphism. In the African *Papilio dardanus* there are several female morphs, each resembling a different, chemically protected species, so reducing apparent density (Sheppard, 1975). The Oriental *P. memnon* has three morphs in each sex (Richards and Davies, 1988). In a lesser-known case, the Neotropical *P. torquatus*, two polymorphic forms resemble those of poisonous *Papilio* spp. (D'Abrera, 1981).

In *Müllerian mimicry,* a group of distasteful or dangerous species evolve a common warning colour and pattern for mutual advantage: they have a similar *advertising style*. Batesian and Müllerian systems have evolutionary consequences for *all interactants*. For efficiency in the former, the mimic should be much rarer than its model and have a phenology lagging just behind it. But when the model is an insect, it too may suffer increased predation since it may be confused with the palatable mimic. In effect, trans-specific predation occurs (see Section **10.2.3.9**). So a premium exists on its evolving a different pattern. But when the model is a tetrapod face (see above) this effect will not occur: little birds do not prey on alligators! In Müllerian guilds, there is an evolutionary convergence towards closer resemblance, so *increasing* joint density and mutual protection: an effect opposite to that in cryptic polymorphism. In three *Heliconius* butterflies in Costa Rica, hybrids having novel wing patterns are subject to greatly increased predation (Kronforst *et al*., 2006).

Aggressive mimics, either predators or parasitoids, use deception to get close to their victims, as they may be confused with conspecific individuals (Sections **8.2.2.3(c)**, **8.2.2.5(e)**, **8.2.2.5(g)** and **8.2.2.5(s)**). While mimicry and crypsis both involve natural deception, crypsis has no outcomes for the object mimicked. So, the two systems should not be combined (Cott, 1940; Vane-Wright, 1980; Berry, 1985). Deception is *perceptual exploitation*, or better 'the exploitation of perceptual biases' (EPB) (Schaefer and Ruxton, 2009; see Merilaita, 2003). Traits evolve in the sender exploiting perceptual biases of the receiver. EPB aids our grasp of the initial stages of cryptic and mimetic evolution. Of course, chemical deception (Dettner and Liepert 1994; Chap. 8 of this book) has similar imperatives and works in the dark (Section **10.1**). For insects at least, with their developed chemosensory systems, such deception will likely prove to be at least as general as that depending on reflected light, and should be looked for in dark places (Section **8.2.2.4(l)**). In all deception a premium exists on novelty. Good crypsis reduces the predator's rate of finding prey (Merilaita, 2003), so at some point searching is no longer cost effective. Finally, Mallet (1995) regards 'mimicry' as 'a bad term because it superimposes an evolutionary explanation on a morphological description'. But later he effectively recants as in most cases 'mimicry seems virtually the only explanation'.

10.2.3.6 Survival: Physical factors: Mechanical factors

These are often neglected in ecology, perhaps because they can be catastrophic, unpredictable and hard to investigate. They contrast with temperature and humidity, which can be quantified as a dose having intensity and duration, in that there may be a single destructive event. But this is no reason for omitting them in a synthesis. Their effects are diverse: mildly energetic factors tend to be favourable, highly energetic ones unfavourable. Insects often employ moderate winds for migration and resource finding. But storms, made up of wind and water in highly energetic states, are *catastrophic*, their avoidance being a prime element of life-history strategies (Section **9.7** and **10.2.4.1**). Convectional storms occur commonly in the seasonal tropics and towards the centres of continents. We noted another combination in Section **10.2.3.4** when high temperature, low humidity and wind increase the drying power of the air. In agriculture, tillage (Section **13.2.3.5(a)**) is a mechanical means of destroying pests in the soil either directly, or indirectly by exposing them to desiccation and/or avian predation.

The mechanical effects of heavy rainfall and/or hail, often with strong winds, may kill insects. In paddies, pest Hemiptera are frequently dislodged, drop into the water, and drown. It is a common hazard for exophytic feeders and recorded for many aphids. *Sitobion avenae* often fall to the ground under cereal crops, becoming prey to carabid beetles such as *Agonum dorsale* and to linyphiliid spiders that spin ground webs (Winder, 1990). For *Bemisia tabaci* on cassava in Uganda, dislodgement, often due to heavy rain, is a major cause of nymphal mortality (Asiimwe *et al*., 2006). Chrysomelid larvae seem particularly vulnerable since, unlike caterpillars, they lack abdominal legs to grasp the leaves. Larval Colorado beetles often succumb like this (Harcourt, 1964). Even lepidopteran larvae are killed by storms (Harcourt, 1969; Denno and Benrey, 1997), while in Australia, eggs and young larvae of *Heliothis* on cotton are often killed in this way (Fitt, 1994).

Not only do large-scale mechanical factors affect insects directly, but also the general environment (Section **10.1**). They include catastrophic events like earthquakes, tsunamis, hurricanes and tornadoes, which are essentially unpredictable. High winds strip leaves, break branches and uproot trees, making food for herbivores scarce but leading to its superabundance for detritivores. After Hurricane Gilbert hit Jamaica on the 12 September 1988, in which local winds exceeded 250 km/h, not a single leaf could be found on most trees and many exotic species were uprooted. I was there at the time. Thus, hurricanes increase light penetration in forests. Driven leaves pile up, smothering herbaceous plants, and then rot, killing them and many insects. High winds with heavy rains destroy trees, especially shallow rooted conifers. Hail stones cause general physical damage. Torrential rain is a source of great destruction, causing erosion within high-gradient streams, flooding of low levels and landslides on sloping ground. Here we see dramatic interactions of the topographical, physical and biotic environments. Such violent events also kill larger animals, producing extra food for the insects that eat their carcasses. But people, employing mechanical means, also cause catastrophic destruction as far as insect habitats are concerned. Clear felling of forests is a prime example, and subsequent effects of this, among others, have been studied on the spatial dynamics of the butterfly *Euphydryas editha* (Thomas *et al*., 1996). Indeed, such events are commonplace for pest insects in agriculture when crop rotation is used.

On a calmer note, seasonal winds blow at predicable times and directions in many parts of the world. Some species have adapted to them, using such advection (Section **2.2.2.1**) to assist migration. Thus seasonal movements of the beet leafhopper, *Ciculifer tenellus*, in the San Joaquin and Sacramento Valleys relate to predicable seasonal and diurnal winds, as do similar migrations of some *Pieris, Pontia* and *Vanessa* butterflies in Europe. While these winds assist movement they entail great mortality for migrants (Southwood, 1988; Section **10.2.5.1**). Light winds, however, assist in finding food and mates locally by olfaction (Section **10.2.4.1**), in turn affecting RS. In deep gullies the topographical modification of weather is extreme. They are cooler since insolation is reduced, the soil remains drier in sheltered areas and while the wind blows in only two directions, it can be strong and carry dust. Dust has destructive effects on insects by abrading the waxy surface of the cuticle (Rosenheim, 1998; Section **10.2.3.4**), especially since dust storms often occur at those critical times when insects are stressed for moisture. Traditionally, some people in Africa mix dusts with grain to help deter pests (Section **13.1.3**).

10.2.3.7 Survival: Biotic factors: Population density

Here we deal with primary effects of density (Section **10.1**), for secondary effects in relation to enemies see Section **10.2.3.9**. Both negative and positive influences on survival can occur at low and at high density. At low density or in small groups the Allee effect (Section **10.2.2.4**) often causes a breakdown of co-operation in siblings or family groups and reduced survival. The establishment of a nest by social insects is most likely to fail when only a few (related) females are present, mortality being inversely density dependent. Then, in adult bark beetles (unrelated) such as *Dendroctonus* colonizing pines (Section **4.2.1.2(h)**), only mass attack, using an assembly pheromone, overcomes resin flow. Allee effects also have outcomes in the general lack of success of small, invading populations (Williamson, 1996; Liebhold and Tobin, 2008), ones that are exacerbated if their drive to redistribute is maintained. So as with growth, survival is often highest at some optimal, intermediate density. Allee effects are embodied in the dis-operation parameter *q* in Southwood and Comins' (1976) population model (Section **11.2.2.5**). Positive effects of low density are generally the obverse of those causing negative effects, namely resource abundance, avoidance of pollution and reduced defences in plants or victims. When high density improves survival it is often due to better defence (Section **10.2.3.9**). But there is no universal optimum density for a given species. Complicating factors include the instar involved, food availability (Thompson, 1929) and the unit of space: patch, habitat or landscape, to which density refers (Section **12.2**).

At high density, competition and intraspecific predation (Section **9.8**) may occur. The former results from excessive numbers in relation to resources and often produces various deleterious effects, including poor survival. For a human population, this effect was known as Farr's law (Brownlee, 1919), but following H.S. Smith (Section **11.2.2.2**) is now called density-dependent mortality, which is explicit. Colorado beetle larvae at high density not only cause a shortage of food and limit its production (Section **10.1.2**), but also pollute it. This is embodied in Verhulst's logistic (Section **11.1.2**), the outcome being density-dependent reduction of r_m, the rate of increase (Murray, 1994). As food is the major resource, we now consider high population density in this context.

10.2.3.8 Survival: Biotic factors: Food

Some foods promote rapid growth and development and so enhanced survival, while others do not. Food finding and *egg distribution* by a female and good food selection for the offspring often lead to their enhanced survival (Sections **9.1** and **10.2.5.2**), part of the *preference/performance linkage* (PPL; Jaenike, 1978; Price, P.W., 1997; Clark *et al.*,2012). Both components, however, are hard to estimate in the field (Thompson, 1988). While evidence exists for PPL in some species that lay directly on the food (Ohgushi, 1998), in others it is clear from the mode of egg distribution that this cannot be so. Species that deposit all the eggs in one batch away from the food (bagworm and gypsy moths), and those that scatter them with abandon (*Callimorpha dominula*; Goulson and Owen, 1997), swift moths and some parasitoids (Section **8.2.2.5** and **10.2.5.1**), will not show the link. However, some insects that lay eggs away from plants, like *Dermolepida* (Section **3.2.1.2(b)**), show a PPL related to soil quality.

But in two leaf miners, *Phytomyza ilicis* (Valladares and Lawton, 1991) and *Tischeria ekebladella* (Gripenberg *et al.*, 2007) where PPL is expected, careful work does not show it. Harvey *et al.* (2015), while finding the link, unearthed complexities when applying it to three hyperparasitic *Gelis* spp. Then in the thelytokous weevil *Otiorhynchus sulcatus* (Section **3.2.1.2(c)**), parent/offspring conflict (Trivers, 1974) has greater explanatory power than PPL (Clark *et al.*, 2012). Also, if several females select adjacent high-quality plants, the ensuing high joint density of progeny might attract mortality due to an aggregative response from enemies, and/or stronger defences from the plants. Egg clumping also counters risk spreading (Section **9.7**). But insects may thrive in culture on plants that they do not select in nature (South, 1920/1923; Dethier, 1954), while Levins and MacArthur (1969) imply that monophagy can be a time-saving strategy, like Lovell's rationale for oligolecty (Section **2.4.1** and **8.2.1.1**).

Recall (Section **2.4.2**) that much plant food is protected biochemically, not only by low quality but also by secondary compounds (Fraenkel, 1959). Oligophagous insects can detoxify their chosen food and often the chemical defences of related plants, but generally survive poorly on the latter. But many exophytic herbivores turn these defensive compounds to their own use, so exchanging a negative for a positive outcome. Sequestered poisons are used against enemies, another aspect of food affecting survival as well as growth. Such insects often advertise their harmful nature by warning colours and patterns (Sections **5.2.1** and **10.2.3.5**), and diverse *indirect effects* may exist (Thompson, 1929; Ohgushi, 2005, 2008). Less obviously, some caterpillars and other exophytic herbivores use sequestered secondary compounds that *kill or deter endoparasitoids*, so improving their own survival (Cheng, 1970; Werren *et al.*, 1992; Karban and English-Loeb, 1997; Sime, 2002; Singer and Stireman, 2003; Zvereva and Rank, 2003). Ectoparasitoids would be less affected. While there is much current research, Flanders (1942) and Smith (1957) describe such effects for scale insects. We treat the subject here since (i) it affects host/parasitoid models and (ii) some workers (e.g. Ives, 1991; Barari *et al*., 2005) still believe that parasitoids always kill their hosts. Potential hosts also use other means to destroy parasitoids.

Winter moths develop most rapidly on oak, and when *Lypha dubia* (Tachinidae) attacks the larvae on this tree (Section **5.2.1.4(g)**) its progeny are encapsulated more frequently than on other tree species (Cheng, 1970). When *Manduca* larvae feed on tobacco the nicotine hardly reduces their growth, but causes significant mortality in their parasitoid *Cotesia congregata* (Barbosa *et al*., 1991). Polyphagous gypsy moths provide a similar case (Werren *et al*., 1992). In another moth, *Grammia geneura* (Arctiidae), the mean mass of female pupae from larvae on *Malva* (Malvaceae) is greater (63 mg) than those on *Ambrosia* (Compositae) (35 mg) (Singer and Stireman, 2003; Karban *et al*., 2010). But when *Exorista mella* (Tachinidae) parasitizes the larvae, 80% of those on *Ambrosia* overcome the attack, but only 53% of those on *Malva* do so. If parasitism were high it would pay a female to choose *Ambrosia* food if available. For three *Pieris* spp. in Japan, the choice of cruciferous food plant has a big influence on field percentage parasitism (Ohsaki and Sato, 1994). Here we expect the AF of host's surviving attack to be reduced (Section **10.2.5.7**), namely a trade-off between survival and fecundity (Singer and Bernays, 2003), a sequential action between two attributes needing further data. But it would be well to distinguish between deterrence, as in Sime's *Battus* larvae (Section **10.2.3.5**), from actually killing the parasitoid.

There are several other cases of a potential victim's food deterring its enemies. Sub-optimal food may confer a lesser risk of predation (Rowell-Rahier and Pasteels, 1986, in Leather and Awmack, 1998). In many Neotropical caterpillars, oligophagous species are more repellent to predatory ants than are those of polyphagous species (Dyer, 1995). Gypsy moth larvae fed on oak and maple foliage are more resistant to baculoviruses than those on poplar or pitch pine (Keating and Yendol, 1987). Adult herbivores may also contain poisons derived from the food when juvenile, protecting them from predation, as in *Zonocerus* grasshoppers (Section **5.2.1.1(f)**), Colorado beetles (Section **5.2.1.2(c)**), monarch butterflies, and cinnabar and burnet moths (Dempster, 1982). But herbivores use plant products for other means of survival. The larvae of some hawk moths use carotenoids from their leafy food to synthesize green cuticular pigments matching it (Grayson *et al*., 1991). So, plant chemistry mediates interactions between herbivores and their enemies. But despite such defences, exophytic larvae and pupae are attacked by more enemies and suffer higher mortality than endophytic larvae (Cornell and Hawkins, 1995), while successful defence may result in reduced AF, as above.

Food for detritivores originates diversely through the trophic spectrum (Section **8.2.4**), but it is always undefended intrinsically. *Phytodetritus* from plants is widely distributed. It has low nutritive quality, hence the growth of insects consuming it is usually slow and mortality factors have a long time in which to act. It also contains microbes that affect survival because they are pathogens or symbionts (Section **10.2.2.6**). Dead tree trunks, while localized, take years to rot away and so provide long-lasting patches (Hamilton, 1996). But dead food of animal origin, either *coprodetritus* or *zoodetritus*, is localized and ephemeral. Being nutritious, it attracts many potential competitors and enemies (Trumbo, 2016). Some dung beetles combat this by rolling balls of their favourite baby food to a safe distance before burying them (Bartholomew and Heinrich, 1978). *Nicrophorus* beetles inter small carcasses and defend them from enemies. Although *Calliphora* larvae may die through intraspecific competition and predation from other maggots (Hanski, 1987), vertebrate scavengers are a major threat (Putnam, 1977). Widely dispersed plant detritus carries no such risk.

Living animal food (*victims*) presents a direct risk to the survival of *focal predatory and parasitoid* species because it is defended, often by physical and chemical means. Since such enemies usually attack several victims during their life, each event may entail a risk of physical damage and of poisoning. Potential hosts of parasitoids frequently defend themselves physically, for example *Acyrthosiphon pisum* adults against the parasitoid *Aphidius ervi* (Ives and Settle, 1996). Hosts often kill larval endoparasitoids by encapsulation (Section **8.2.2.5**, see also above). But apart from the risk they engender, prey may be in short supply. In two carabid species, food shortage in autumn resulted in lower survival during winter, since the fat bodies the beetles metabolize to survive were smaller (van Dijk, 1994).

10.2.3.9 Survival: Biotic factors: Enemies

Throughout their life focal individuals are to a variable extent at mortal risk from a series of enemies, a risk that can be quantified in a life table (Section **11.4.1**). Recall (Section **10.2.3.1**) that the chance of passing from egg to adult is small, often <0.1. For herbivores, enemies are the major cause of juvenile mortality (Cornell and Hawkins, 1995). While in harsh environments physical factors kill many individuals, usually irrespective of population density, the risk from enemies, especially entomophagous insects (Section **8.2.2**), is often related to this density (Section **10.2.3.7**), the classical *density-dependent mortality* (Section **11.1.2**), here a *secondary effect of density*. High densities entail greater risk since enemies spend less time searching and more time finding as victims are close together. Then, the energetic cost of searching is less than the rewards of finding. Optimal foraging models (Charnov, 1976) predict that predators in unfruitful patches, generally because of low prey density, should soon give up searching. But when there are few enemies and the individual is one of many, not one of few, it may have less chance of being attacked, resulting in *inverse density dependence* (Section **9.9**). Spruce budmoths (Section **5.2.1.4(c)**) provide a well-researched example. This situation explains why some small marine fishes exist in massive shoals. Here, peripheral fishes are at greater risk and core ones protected by them (Williams, 1966; Hamilton, 1971). Each fish has a chance to seek safety in the centre. Apart from mobility, this recalls the case of the huge egg masses laid by gypsy moths (Section **5.2.1.4(f)**), where surface eggs protect the inner ones from parasitism by *Ooencyrtus*. Inverse density dependence also results from the congregation of sibling juveniles. Young nymphs of *Nezara* (Section **6.3.2.1(a)**) and young larvae of *Perga, Lymantria* and *Tyria*, arising from egg batches, form sibling groups, functioning to reduce mortality from enemies (Dempster, 1982; Danks, 2007). Outbreaking moths in Canadian hardwood forests often have gregarious larvae. Hunter (1991) showed that this reduces mortality more frequently than expected in a random sample of all moths from these forests.

An insidious problem often occurs in assessing mortality due to field predation, because enemy presence may cause rapid dispersal of potential victims. So, unless sampling embraces the ambit of escape, losses due to predation will be confounded with those due to dispersal, which recalls the case in *Tipula* larvae (Section **9.3**). Thus dispersal occurs when micryphantid spiders attack patches of *Spodoptera litura* larvae (Nakasuji *et al.*, 1973). Like effects occur when the spider *Chiracanthium* attacks *S. littoralis* aggregations on apple foliage (Mansour *et al.*, 1981), when spiders feed on groups of *Nezara* nymphs (Section **6.3.2.1(a)**) and when *Polistes* wasps forage on groups of *Hypantria cunea* moths. On the Tibetan Plateau, the staphylinid beetle, *Philonthus*, drives its burrowing, coprophagous prey deeper into the soil (Wu *et al.*, 2015). Also, smaller predators may cause more dispersal than mortality, while the opposite can occur with larger ones. In addition, some spiders kill more prey than they consume (Riechert and Lockley, 1984), called *wasteful killing*.

The *disturbance/consumption (D:C) ratio* is a measure of predatory efficiency. It varies widely (see Table 2 in Nelson and Rosenheim, 2006). Thus, larval *Chrysoperla* encountering *Aphis gossypii* ate 96% of them, while the ladybird, *Hippodamia*, ate only 1% of pea aphids. van Dijk and den Boer (1992) regard carabid beetles as inefficient predators. But some libellulid dragonflies capture 65–93% of the prey they chase (Marden *et al.*, 1998). Similarly, solitary wasps are often highly effective. *Sceliphron assimile* can capture and provision each spider in less than 15 minutes (Freeman and Johnston, 1978a; Section **12.3.4.3**), while *Zeta abdominale* takes about 36 minutes to provision each caterpillar (Taffe, 1983). *Trypoxylon monteverdeae* is recorded at an amazing rate of 81 ± 14 sec/spider (Brockmann, 1992). Naturally, prey availability and weather also effect efficiency (Messenger, 1964a; Dreisig, 1981). But *Sphex ichneumoneus* can take a week to collect a cache of around six katydids, while many solitary wasps have difficulty in provisioning large prey when it is windy, and cease doing so if it rains.

This ability of an enemy to search is often not raised although embodied, for example, in Nicholson and Bailey's (1935) classical *area of discovery* (Section **11.5.2.2**) and further discussed by Hassell (1982). But in these models space *per se* is not considered, they are *aspatial*. A mite consuming five insect eggs on a leaf is given the same searching efficiency as a tachinid fly parasitizing five caterpillars on five trees in the same time. Furthermore, models often assume that all migrant enemies find a new patch and hence their victims, whereas there may be great wastage (Danks, 1971b; Freeman, 1973a, 1981a; Freeman and Ittyeipe, 1993). Then the empirical studies analysed are not random samples from the insect fauna, a necessary starting point for conclusions about insects in general. Most refer to species with dense populations. Thus, we are unsure of the existence, status and effects of density dependence in sparse populations (Strong, 1986): the large majority (Section **9.4**). But since pests are rarely sparse, our conclusions may relate to them more closely.

Another factor in predation is the relative sizes of enemy and victim. Some prey are too small to cover the energetic costs of searching and handling, while others are too big to overcome. Also, learning (Taylor, R.J., 1974) and hunger influence the choices predators make. Female ladybirds, *Adalia bipunctata,* consume a maximum of only 10 aphids/day, after which they are satiated (Mills, 1982). Cannibalism among the predators (Sections **9.8** and **10.1.2**), which occurs frequently, adds further complications.

Of course, enemy numbers vary as well as those of the focal species. Most models, which consider a victim/enemy pair (Section **11.5.2.3**), assume that both populations vary together. In nature this is most likely to happen when the enemy specializes on a victim species, shares its living space and has similar relations with physical factors. But since most enemies are generalist (facultative) rather than specialist (obligate) (Godfray and Muller, 1998), live in other parts of the habitat and respond differently to physical factors than focal species, their dynamics are *de-coupled* from those of their victims. This recalls *density vague* dynamics (Strong, 1986; Section **11.2.2.4**). When several generalist enemies exploit a victim species (Vinson, 1984; Hawkins, 1990; Hawkins *et al*., 1994) they may interact. *Ostrinia nubilalis* has 15 larval parasitoids in Europe (Thompson and Parker, 1928a), *Acleris variana* (Tortricidae) has 38 in eastern Canada (Miller, 1966) and 76 attack *Zeiraphera diniana* in Switzerland! In the UK, 16 mainly eulophid parasitoids attack *Phyllonorycter platani* (Nash *et al*., 1995) and 37 parasitoids exist over the range of another miner *Cameraria ohridella*, 15 near Vienna and 10 in northern Germany. But their phenology in Western Europe is not synchronized with that of their host (Grabenweger and Lethmayer, 1999; Klug *et al*., 2008). Recently there have been extensive outbreaks. Global warming may have upset established relationships in some cases (van Nouhuys and Lei, 2004; Parmesan, 2006).

The effect of enemies on survival over several generations in the field is also commonly measured by the percentage mortality they cause on varying densities of the victim's population (Section **11.4.4.2**). In the early days of insect ecology there was much speculation concerning the temporal density dependence of this interaction. While laboratory experiments were devised, the results were hard to relate to nature. Latterly, many field studies, chiefly on the action of parasitoids, have been analysed (Lessells, 1985; Stiling, 1987; Walde and Murdoch, 1988). But the assumption of *direct density dependence* is supported in only about one-third of the cases: the higher the victim's density, the higher is its mortality (**Fig. 10.17a**). In about one-quarter of these studies there is inverse density dependence (**Fig. 10.17b**; Price, 1988) and no evidence of any mortality/density relationship in the rest. Reviewing the dynamics of Lepidoptera, however, Dempster (1983) found density dependence in 16 of 22 species. Then, Stiling's results have been questioned (Hassell *et al*., 1989). Hails and Crawley (1992), in an extensive study of the gall-wasp *Andricus quercuscalicis*, found spatial density dependence in only 15% of 62 cases, while ~66% of these were inverse! Contrary to Howard and Fiske's expectation (see below and Section **11.1.2**), avian predation of the gall's contents was consistently, *directly* density dependent. This being said, models by Chesson and Murdoch (1986) indicate that both direct and inverse density dependence would add stability, in the Nicholson–Bailey context (Section **11.5.2.3**), to host populations.

An enemy could operate density-dependently at low victim densities, but fail to do so above a threshold (Morris, 1963; Varley and Gradwell, 1970), the '*release point*' in the Southwood–Comins synoptic model (Section **11.2.2.5**). Conversely, no such mortality might occur *until* a threshold density is reached (McNeill, 1973; Dempster, 1983; Section **12.3.2.3**). These findings have implications for theories of insect numbers (Section **11.2**), but *within generation effects*, such as the *aggregative* and *functional responses of enemies*, must be separated from *long-term population effects* (Sections **11.4.4.2** and **11.5.2.2**(**b**)). The aggregative response means the congregation of enemies in a generation onto a group of victims. The functional response is the attack rate of an enemy on its victims (Solomon, 1949; Holling, 1959a) and may relate to the latter's population density (Hassell, 1978; see below). In the long term, and so with a delay, the changing

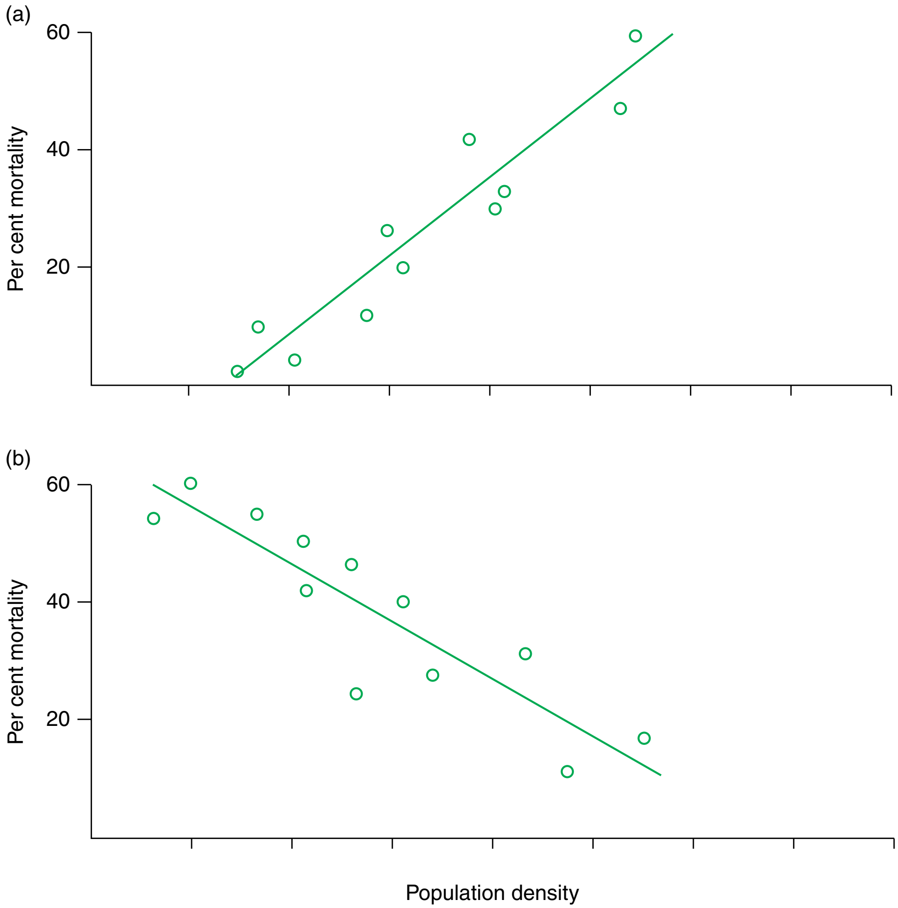


Fig. 10.17. Density-dependent mortality from an enemy: (a) direct and (b) inverse. In (a) there is no such mortality at low density. Data are hypothetical, but see Fig. 11.22.

numbers of the enemy population over time in relation to its changing RS, is the *numerical response*. For each victim killed a fixed number of enemies is produced. This concept is more appropriate for specialist than generalist enemies (Bonsall and Hassell, 1997).

Holling (1959a) classified three types of functional response: (i) linear up to a plateau; (ii) rising at a declining rate; and (iii) sigmoid (**Fig. 10.18**), but several functional types have been modelled recently (see Table 4 in Turchin, 2003). In the ichneumon *Nemeritis*, learning materially affects the shape of these curves and may stabilize the system (Taylor, R.J., 1974). Price (1997) lists five factors on which coupled dynamics depend, which I have reworded slightly: (i) an individual's functional response; (ii) increased reproduction in the enemy's population; (iii) increased immigration; (iv) the developmental response; and (v) the enemy's functional response to its own population density. These constitute the '*total response*' of enemies to increasing prey density. But we note that the amount of immigration, the aggregative response, is contingent on an enemy's ability to search (ISC; Section **10.2.4.1**) as well as on the proximity of its victims and its numbers at source.

While the surveys above suggest that direct density-dependent mortality occurs in a minority of natural cases, such processes are held by many to be basic to insect dynamics (Hassell *et al.*, 1989; Turchin, 2003). Extrinsic factors, especially weather, may mask their being manifest (Wellings *et al.*, 1985). Thus, temperature is the main driver of the numbers of prey eaten by tiger beetles along

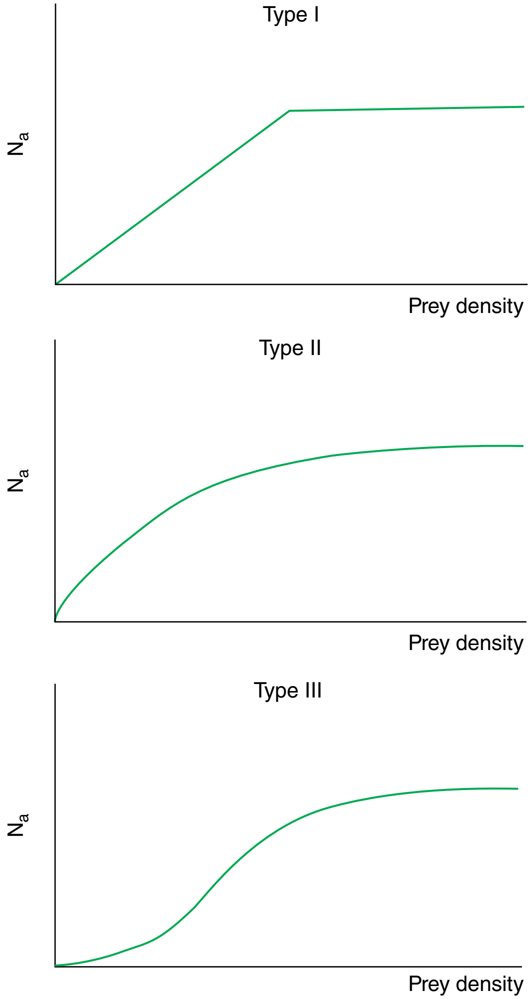


Fig. 10.18. Holling's functional response curves. M. E. Solomon had earlier (1949) suggested similar relationships. From Speight, M.R., Hunter, M.D. and Watt, A.D. (1999) *Ecology of Insects*. Oxford, UK: Blackwell.

a sandy road in Denmark (Dreisig, 1981). But the time-series data analysed are often too short (Hassell, 1998b), the effect may be obscured by habitat heterogeneity (Strong, 1986; Mountford, 1988), or the enemies are inefficient (van Dijk and den Boer, 1992; Polis and Strong, 1996; see above). In the inductive sciences (Section **11.5.1**), however, phenomena must be demonstrated empirically, not left to faith, 'the substance of things hoped for, the evidence of things unseen' (Hebrews 11: 1). We cannot disregard the 'rich anarchy of the evidence' (Hampson, 1990). While theory guides observation, we must not observe with blinkered vision. No one is as blind as he who wishes not to see.

Enemies often mutually interfere (Beddington, 1975), reducing their individual killing rate. This led to the idea that the functional response could be ratio dependent rather than prey dependent (Arditi and Ginzburg, 1989), being contingent not only on prey density $f(N)$, but also on joint density $f(N/P)$ (Abrams and Ginzburg, 2000; Turchin, 2003). But field experiments (Schenk *et al.*, 2005), using tortoise beetle larvae and *Polistes* wasps, revealed that neither assumption described the data well. In a telling study of a superabundant culture of *Acyrthosiphon pisum* (Section **5.3.1.2(g)**), its parasitoid, *Aphidius ervi*, regularly died out (Ives and Settle, 1996). This resulted from a high mortality of parasitized hosts, plus their high and unrelated density-dependent mortality. The growth rate of the parasitoid population was *least* when aphid density was greatest, as in the inverse density dependence shown when ichneumons and tachinid flies attack outbreaking populations of *Choristoneura* (Section **5.2.1.4(c)**). In this connection, some resistant strains of *Ac. pisum* can destroy *A. ervi*'s eggs (Henter, in Gould, 1991). They often contain the bacterium *Hamiltonella defensa*, which helps them combat this wasp (Oliver *et al.*, 2008; Section **5.3.1.2(h)**). Recent research (Asplen *et al.*, 2014), reveals that while *H. defensa* protects *Aphis craccivora* from two *Binodoxys* spp., it has no effect on *Lysiphlebus orientalis* and *Aphidius colmani*. A bacterium modulates interactions of a host aphid and its parasitoids! More complexity occurs in grass-feeding aphids and their parasitoids. In Argentina, rye grass may or may not contain the endosymbiotic ascomycete *Neotyphodium*. In field plots, *Rhopalosiphum padi* and *Metopolophium festucae* (Section **5.3.1.2(h)**) were threefold denser on grass lacking this symbiont, while rates of total parasitism involving seven species were much higher, and hyperparasitoids were numerous (Omacini *et al.*, 2001).

Potential victims kill their parasitoids frequently, often employing defensive compounds from plants or endosymbionts to do so (Section **10.2.3.8**). Similar species, however, vary in this ability. *Blaesoxipha atlanis* (Sarcophagidae) attacks several grasshopper species on the Canadian prairies. But while *Melanoplus bivittatus* and *M. packardii* using encapsulation and melanization always kill these parasitoids, *M. sanguinipes* and *Camnula* *pellucida* kill few of them (Danyk *et al*., 2005b). In Kansas prairie, the grasshopper fauna shows great variation in levels of parasitism by Diptera (Laws and Joern, 2012). Then in gregarious parasitoids, small larval broods often fail entirely, being unable to combat the host's defences.

When two victim species breeding in proximity have a common enemy, their dynamics may be affected (Nicholson, 1933; Freeman, 1973a, 1974, 1982; Stenberg and Hambäck, 2010), the outcomes often differing between them. While Williamson (1957) said: '… two victim species are in competition when they are both controlled by the same enemy', this is in no way resource competition (Section **9.8**). Rather surprisingly, it has been called *apparent competition* (Holt, 1977; Lawton, 1986; Holt and Lawton, 1994), perhaps because the numbers of one or both species are depressed. To their credit, Wäckers *et al*. (2007) define such an interaction as '… a negative effect of one species on another species mediated through [the] action of shared natural enemies'. No scarce resource is involved. *Apparent competition* is ambiguous recalling the broad and nebulous concepts of Nicholson and MacArthur. Bonsall and Hassell (1998), also to their credit, regard its use as 'colloquial'.

'Apparent' has two meanings: (i) visible, plainly seen, conspicuous, evident, as used by Feeny (1976; Section **2.4.1**); and (ii) seemingly, contrasted with real, which may be Holt and Lawton's meaning. *Competition must always be defined* (Section **9.8**); shown not assumed (Park, 1954; Birch, 1957; Lawton and Strong, 1981). Then, Hespenheide (1991, p. 544) uses Holt's term ostensibly without knowing Holt's meaning! The effect, which I term *trans-specific mortality*, is probably commonplace (Freeman, 1974, 1977, 1982; Bonsall and Hassell, 1997; Chaneton and Bonsall, 2000; Stenberg and Hambäck, 2010), as the big, welcome review of life tables by Cornell and Hawkins (1995) suggests. This counters Schoener's (1984) assertion that we have no 'evidence that competition is more intermittent than predation'.

Trans-specific mortality is a major component in the ecology of Jamaican solitary wasps from which it was first described (Freeman and Parnell, 1973). The major mortality factor on juvenile *Sceliphron*, *Melittobia* (Section **8.2.2.5(p)**), is spatially density dependent (Section **11.4.4.2**). But several secondary wasps breed subsequently in *Sceliphron*'s disused mud cells and *Melittobia* parasitizes them too. The crucial point is that an enemy that has been building up its numbers on one victim species *transfers* to a subsequent, usually related, victim species. For these secondary wasps, the level of mortality is determined less by their own density, more by the level incurred by *Sceliphron* at the same site (Fig. 10.19; see also Fig. 1 in Freeman, 1974, and Fig. 1 in Freeman and Jayasingh, 1975a). While this too is a lateral effect (Section **10.1**), it *has nothing to do with resource competition*. But let us be clear: if two parasitoid individuals were to

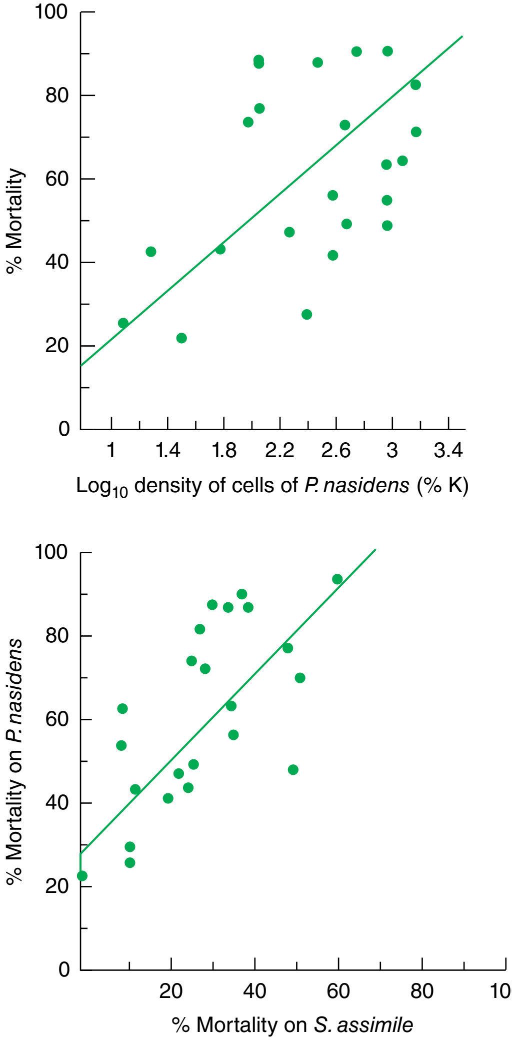


Fig. 10.19. Trans-specific mortality in *Sceliphron* and its inquilines. Adapted from Freeman (1974) *Carib. J. Science* 14, Fig. 1, and Freeman and Jayasingh (1975a) *Oikos* 26, Fig.1B. Reproduced with permission.

attack the same host individual (the resource), true competition might well occur, as Nicholson pointed out originally (Section **11.2.2.2**).

Trans-specific mortality may also occur in the dynamics of two *Sceliphron* spp. in Trinidad (see Fig. 4 in Freeman, 1982). Where *S. asiaticum* and *S. fistularium* nest at the same site they do not compete, but their percentage mortalities from *Melittobia* are correlated ($r = 0.62$, $P < 0.05$), *S. asiaticum* with its less robust cells has the higher mortality (Fig. 10.20). But here parasitoids that may *not* have had origin in one species also attack our focal species. *Trans-specific mortality may be partial*. Then recall that three *Pieris* spp. in Japan show different levels of defence against *Cotesia* (Sections **5.2.1.4(k)** and **10.2.3.8**). Muller and Godfray (1997), for two aphid species feeding on different but adjacent plant species, found linked predation from a coccinellid beetle and subsequent effects on a suite of braconid parasitoids. Indeed, when *Aphidius ervi* (Section **8.2.2.5(m)**) moves between and parasitizes its several aphid hosts (*Sitobion, Acyrthosiphon, Metopolophium*), not only does its RS vary with host species, but it is also affected by its previous host (Powell and Wright, 1988). *Melittobia's* AF depends on *the size* of its many host wasps. When *Asecodes mento* (also Eulophidae) attacks the chrysomelid beetles *Galerucella tenella* and *G. calmariensis,* its sex ratio and female size are different in the two hosts (Stenberg and Hambäck, 2010).

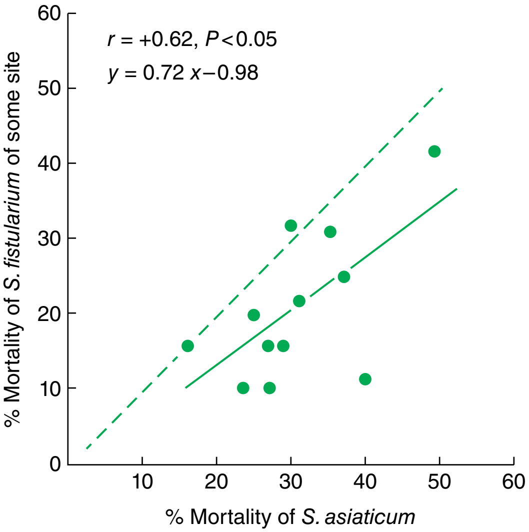


Fig. 10.20. Trans-specific mortality for *Sceliphron asiaticum* and *S. fistularium* in Trinidad. *Biol. J. Linn. Soc.* 17 (1982) Fig. 4, p. 352. The plot may not be due entirely to trans-specific effects, but shows that *S. fistularium* is better defended against *Melittobia* than is *S. asiaticum.*

Other probable cases of trans-specific mortality concern two leaf hoppers, *Dikrella cruentata* on blackberries and *Erythroneura elegantula* on adjacent wild grapes, where both bugs share the egg parasitoid *Anagrus epos* (Section **5.3.1.2(a)**). Two moths, *Operophtera* and *Tortricodes* on oak in the UK, share the tachinid fly *Lypha dubia* (Cheng, 1970). The tortricid complex on apples shares the eulophid parasitoid *Colpoclypeus florus* (Blommers, 1994). Such mortality may be involved where *Chilo partellus* is ousting other stem borers in East Africa (Kfir, 1997; Section **4.4.1.1(c)**) and has been found between two parasitoids that share a hyperparasitoid (van Nouhuys and Hanski, 2000). Chaneton and Bonsall extend this concept to two plant species consumed by a common herbivore, while reflection reveals that in parasitology, anthroponoses and zoonoses are comparable, as both primary and secondary hosts often suffer from the common parasite (Dye, 1992; Section **7.3.2.4(d)**).

So, when two species living together share a common enemy affecting their dynamics, the term *trans-specific mortality* (and hence *trans-specific parasitism*, *trans-specific predation*, and even perhaps *trans-specific herbivory*) is preferable to the nebulous '*apparent competition*'. These terms refer to observable behavioural processes, not to a negative outcome of doubtful cause. Models (Abrams and Matsuda, 1996), under certain conditions, predict an *increase* in the densities of both prey species, usually because of prey switching or predator satiation (Murdoch, 1969), namely a beneficial outcome of competition! Such findings and others with two or more parasitoids competing for a scarce resource, namely a single host species (Freeman and Geoghagen, 1989; Yu *et al.*,1990; Section **10.2.3.10**), show great complexity. They have been discussed theoretically (Hassell and May, 1986; Bonsall and Hassell, 1997, 1998) and analysed by Holt and Lawton (1994). But for species with itinerant behaviour, such as many *Pieris* butterflies, using such equations is inappropriate.

As noted above and long ago by Howard and Fiske (1911), high population density of a victim may lead to *reduced* proportional predation. This can result from its rate of increase out-stripping that of its enemies, an effect often seen in dense populations of aphidid and psyllid bugs. Or it may be caused by the sudden emergence of great numbers of adults, as in crane flies (Freeman, 1968), some *Simulium* and mayflies (Corbet, 1964; Sweeney and Vannote, 1982) so satiating predators, another aspect of a temporal refuge (Section **9.9**).

Apart from enemy insects, our species may be attacked by a wide range of other organisms (Sections **8.2.2.6** and **12.3.2.3**), including vertebrates, spiders, nematodes and microbes. Among the latter, the α-proteo-bacterium *Wolbachia*, discovered in 1924, has unusual effects on the survival of many insects (Werren and Windsor, 2000; Jansen *et al*., 2008). It passes vertically to future generations only in the egg cytoplasm, preferentially destroying males (Werren, 1997; van Vugt *et al*., 2009), skewing the sex ratio towards spanandry and in extremes towards female infertility (Section **10.2.5.7**), and can have further complex effects. It has several strains, is present in many insects (Werren and Windsor, 2000), affecting >60% of them (Bordbar *et al*., 2014), and in filarial worms. But apart from its deleterious effects, it may assist insects to fight parasitoids (Sections **5.2.1.2(f)** and **10.2.3.8**). It can also spread between species, often with a mutual parasitoid acting as a vector (Batista *et al*., 2010). In some ladybirds, a *Rickettsia* (Majerus and Hurst, 1997), which is related to *Wolbachia*, and also a spiroplasma (Section **8.2.2.4 (e)**), kill males. Interestingly, all the bacteria causing female bias and cytoplasmic incompatibility, manipulating their eukaryotic hosts, are related (Stouthamer *et al*., 1993).

10.2.3.10 Survival: Biotic factors: Other organisms: Interspecific competition and predation

Interspecific competition (Section **9.8**) may result in a suite of negative effects on RS. They may be trivial or cause slower growth (Section **10.2.2.4**), where in severe cases development takes longer, leading to negative Williams' effects (Section **10.2.2.1**). Here the action on survival is indirect. Of course, the lack of quality food *per se* (Section **10.2.3.8**) is comparable. But more dire outcomes, often when competition is for nutritious, localized food, may lead directly to the death of the contestants and *interspecific predation between erstwhile herbivores and detritivores* may ensue. When the food is a plant, caterpillars are often involved, when it is detritus or dung, flies and beetles are often involved. Within a carcass *Calliphora* and *Chrysomya* spp. often compete (Section **7.4.2.2**), and in South Africa *Ch. albiceps* can be a facultative predator of other maggots (Richards *et al*., 2009).

Competition can result when two or more parasitoid species attack the same host (Askew, 1971; Askew and Shaw, 1986). Thus, in the gall midge *Asphondylia,* four ectoparasitic wasps, *Heterolaccus* and *Calorileya* (Pteromalidae), *Eurytoma* (Eurytomidae) and *Torymus* (Torymidae), compete by scramble for host larvae within the galls (Freeman and Geoghagen, 1989). As enemies, they caused midge mortality, but great attrition among themselves due to interspecific predation. Small parasitoid larvae, sticking to the exterior of larger ones, seem more effective assassins. Similarly, in aspen miners, *Lithocolletis*, competition often favours smaller larvae (Martin, 1956). But for *Asphondylia*, *Trichoptilus* caterpillars (Pterophoridae) eat the flowers, seeds, galls and their insect contents indiscriminately. The moth is a competitor and a predator. In folivores competition may occur between munchers and miners, the latter generally losing (Section **5.2.2**). When a single *Manduca* larva (Section **5.2.1.4(h)**) steadily consumes an entire tomato plant, the fate of *Liriomyza* larvae mining the leaves is bleak from competition and predation, which brings the idea of *asymmetrical interactions* to mind.

Interspecific competition has been assumed to cause exclusion of one species by another, and called Gause's hypothesis (Gause, 1934), Gause's axiom (it is clearly a postulate; Section **11.5.1**) or the '*competitive exclusion principle*' (Hardin, 1960), and so structures communities (Connell, 1983; Denno *et al*., 1995; Section **11.5.2.2**). It is often assumed, since for some workers omnipresent competition is a paradigm (Sections **9.8** and **10.2.3.4**), that if two species using the same resource in the same place show changes in numbers this is *necessarily* the result of competition (Tilman, 1987). Of course, changes in numbers are due *to alteration in the balance of birth and death rates and of immigration and emigration* (Hanski, 1985), as in the BIDE model (Section **11.5.3**). Only if competition can be shown to tip these balances can competitive exclusion be demonstrated.

When investigating interspecific exclusion, three questions must be asked. (i) Does resource competition, defined in Section **9.8**, occur? (ii) Does it have negative effects on the RS of one or both species? (iii) Are these effects sufficient to cause exclusion of the inferior competitor? Patten (1961), in an erudite paper, considers a cybernetic model of such competition, concluding that an 'overwhelming variety' of interactions is possible, even coexistence. For herbivorous insects, Denno *et al.* (1995) found that competition had been shown in 76% of the 193 cases covered, although in these numerous papers it would mean different things to different authors! The effect was frequent in closely related species, as Darwin (1859) postulated, but also in those with sucking mouthparts and in concealed feeders. We note that both the latter groups tend to concentrate on a local resource. In herbivores, competition is often mediated through effects on the plant. A species feeding on the roots may have negative effects on the nutrition of another feeding on the foliage (Moran and Whitham, 1990; Bezemer *et al.*, 2003), and it may be asymmetrical, with one species suffering more than the other. Apart from herbivorous insects, interspecific competition may be critical in structuring communities of parasitoids (Askew and Shaw, 1986). Then, such competition can have different outcomes at local and regional spatial scales, while local and regional time scales are also critical (Hanski, 1983).

Despite biases in selection of experimental material, in that abundant species are often chosen and competition sought actively, *interspecific competition may be on occasion an important factor in insect survival* and probably in structuring of *some* communities. But note Hinton's (1973) advice '... people do not engage on experiments *in vacuo* but only to verify or falsify some preconceived notion'. Great variation exists, however. In an extreme case two species feeding on a plant may have positive effects on their mutual RS (Masters *et al.*, 2001), a possibly evolved accommodation. In *Craspedolepta subpunctata* and *C. nebulosa* (Psyllidae), individuals of both bugs tend to be larger when found together on their common *Epilobium* food plant (Bird and Hodkinson, 2005; Section **12.3.4.2**), suggesting both prefer more nutritious plants and arguing against competition. A similar situation exists in two *Sceliphron* species in Trinidad (Freeman, 1982). The bark beetle *Dendroctonus frontalis* and the cerambycid beetle *Monochamus titillator* in pines in the southern USA provide a complex illustration of competition. Only if *D. frontalis* kills the tree can *M. titillator* complete development (Coulson *et al.*, 1976), recalling the situation between some defoliators of conifers that later facilitate attack by bark beetles. But both beetles then compete in parts of the affected tree.

10.2.4 Movement: Redistribution, resource seeking and escape

10.2.4.1 General introduction

Locomotion is a basic property of animals. Although sessile stages exist (Section **1.3**) we are not concerned with them here, and while plants lack locomotion they employ a moving medium or agent to disperse their products (Section **8.2.1**). Even so they are not simple, having immensely complex defences (Section **2.4.2**). Movement usually involves locomotion as an essential part of insect behaviour. But as opposed to staying hidden it may lead to increased risk, one, however, necessary for carrying out normal activities. Overall, it covers undistracted *redistribution* (Section **9.5**) and ends-directed *seeking* favourable microclimates, resources and refuges, avoiding enemies and facilitating defence. Among terrestrial invertebrates, pterygote insects are unrivalled in their mobility (Section **1.2**), the volant adults operating on spatial scales far greater than those of the juveniles. Like birds, they use fully the three-dimensional structure of their environment, their behaviour being adapted to its graded spatial scales (Endler, 1992; Collett, 1996; Marden, 2000). Flight has evolved to be rapid and energy efficient (Johnson, 1969; Roland and Taylor, 1997). Using diverse movements, insects alter their own density and distribution (Taylor, 1984), a mode quite separate from births and deaths, the NDA (Section **9.3**), and *one fundamental to their dynamics*.

For migration, the prodigious distances adults may fly are revealed by discovering them many kilometres from their breeding habitats, as in *Simulium* (Section **7.3.2.4(h)**), or high in the air (Berland, 1935; Glick, 1939; Freeman, 1945; Pedgley, 1982; Drake and Gatehouse, 1995; Gatehouse, 1997). Movements *en masse* assist our tracking them, but now we can follow *individuals* of medium-to-large size using portable harmonic radar (Boiteau and Colpitts, 2004) and vertically pointing beam systems (Reynolds *et al.*, 2008). Dipole tags weighing only 20–30 mg have been developed which can be tracked by harmonic radar (Gui *et al.*, 2011), which should be suitable for close range tracking. Various marking methods are also available (Southwood and Henderson, 2000). But flight mechanisms are diverse (Sattler, 1991; Brodsky, 1994; Dudley, 2000, 2001). Escape movement is typically local, and with some exceptions such as blow flies, sphingid moths and some pierid butterflies (Section **5.2.1.4(h)**), resources are sought on much lesser spatial scales than those involved in redistribution.

To expand a little: insect locomotion has been variously classified (see, for example, Johnson 1969; Dingle, 1996), and others have treated its dispersive aspect mathematically (Taylor, R.A.J., 1978, 1980; Turchin, 1998; Section **11.5.3**). Indeed, the innate complexity of such movement cannot be appreciated without sampling its mathematics. We distinguish three *functional* modes: (i) *redistribution* (Johnson, 1969; Taylor and Taylor, 1977; Taylor, 1986; Section **9.5**); (ii) *appetitive or ends-directed seeking behaviour* (Craig, 1918; Hardie *et al*., 2001); and (iii) *escape* (Eibl-Eibesfeldt, 1970). These functional modes must be distinguished from their ecological results. Thus, escape reactions may lead to reduced population density, as in the case of failed predation by spiders (Section **10.2.3.9**). So, *individual movement* has clear outcomes for *populations* (Gatehouse, 1987; Shaw and Kokko, 2014), including genetical ones (Begon, 1976; Roff, 1986; Sugg *et al*., 1996; Haag *et al*., 2005).

Insect redistribution is of four types (Section **12.3.4.4(c)**).

1. Non-migrant dispersal. This may be the primitive mode, but is often species-specific and may be reduced at the harsh edge of its range.
For types 2–4 migration may be *through* the matrix or at *high levels* above it (Section **10.2.4.5**).
2. Low-level migrants mainly using their own power to navigate *through* the matrix, their ambit depending on size, flight speed and matrix connectivity (Tischendorf and Fahrig, 2000).
3. Small *diurnal migrants* using convection currents to ascend and then move, largely passively, *high above* the matrix. When great numbers are involved, as in aphids, it *results* in an effective resource-seeking strategy.
4. Larger *nocturnal migrants*, often moths, speeding along in jet streams at the temperature inversion layer (Gatehouse, 1997). They often move farther than type 2 insects and can fly on several nights. Rarely there are similar dawn exodus flights (Reynolds *et al*., 2008).

Intermediate cases exist. While much of a population may move only metres a minority go much farther, so markedly effecting gene flow (Slatkin, 1985). *Bemisia tabaci* (Section **5.3.1.2(c)**) has high flying and low-flying forms (Isaacs and Byrne, 1998), while fast-flying *Vanessa cardui* migrate near the ground or high above it (Stefanescu *et al*., 2007).

Endopterygotes usually have two immobile stages, exopterygotes only one. Pupae are usually immobile, but those of some nematoceran flies can move a little, aquatic mosquito pupae having rapid escape behaviour (Section **10.2.4.8**). Immobile stages must combat inimical physical or biotic factors *in situ* as they, unlike the mobile ones, cannot seek safe locations or actively defend themselves. Locating a favourable refuge is a function of the preceding mobile stage, being either itself or parent. So mature larvae seek a suitable site to pupate. Adult males often seek mates, but this is a female role where males have territories. Most fertilized females seek suitable sites for the eggs, hence adult movement, if not for redistribution or overwintering, often leads to reproduction (Section **10.2.5**). Mobile stages in diapause become immobile and so cannot escape from danger (Leather *et al*., 1993).

Nymphs and larvae, then, often show limited displacement by walking, confining them to their habitat, or to their food patch (Southwood, 1988). Notable exceptions are the young larvae of a few moths (bagworms, gypsy moths; Section **5.2.1.4**) that may redistribute appreciable distances in the air on silken threads, an activity further promoted by food shortage. Locust hoppers and armyworms on the ground are juveniles that also travel far, which the unrestricted nature of their habitat permits. Conversely, endophytic larvae and those in the soil have limited mobility since the medium in which they live restrains them. Those of social wasps and bees are confined to cells, those of gall formers to galls, and those of most leaf miners to single leaves. But via the diverse flight strategies of adults, many species have highly mobile populations (Taylor, 1986; Drake *et al*., 1995; Turchin, 1998; Woiwod *et al*., 2001), giving a type of population ecology and genetics in marked contrast to those of other terrestrial invertebrates. Attesting to their frequent flight, several avian families (Apodidae, Caprimulgidae, Hirundinidae, Muscicapidae) and most bats are specialized to catch flying insects.

Migrant insects have undistracted flight preceding egg laying, the '*oogenesis-flight syndrome*' comprising physiological and behavioural components (Johnson 1960, 1969; Harrison, 1980; Drake and Gatehouse, 1995). The longer the pre-reproductive period, the greater the *potential* for migration. While there are exceptions (Section **5.2.1.4(c)**), criticism by a few workers (Baker, 1978; Sappington and Showers, 1992), and males are often marginalized (Shaw and Kokko, 2014), the syndrome is an established feature of insect life (Drake *et al.*, 1995; Dingle, 2001). It is a case of Fisher's Fork (Section **9.7**), the division of metabolic resources *either* to redistribution *or* to reproduction (Wheeler, 1996; Zera and Denno, 1997), the two main functions of adult insects.

I simplify Johnson's (1969) classification of migration here:

1. Emigration *without return* of relatively short-lived adults. This occurs in a wide variety of insects: some bugs, midges, most higher Diptera, solitary wasps and many Lepidoptera. Even so, a subsequent generation may re-migrate.
2. *Emigration and return* of the same individual within its lifetime. This is often found between feeding and breeding habitats, as in some dragonflies like *Anax imperator*, in *Anastrepha* flies and beetles such as *Phyllopertha*.
3. *Emigration and return* migration of long-lived individuals *after adult diapause*, a type found in several cutworm moths that fly to the Rocky Mountains to hibernate and in the Bogong moth (*Agrotis infusa*) that aestivates in the mountains of eastern Australia. The beetles *Brumus* and *Semiadalia* (Yakhontov, 1962) and the bug *Eurygaster integriceps* (Brown, 1965; Schaefer and Panizzi, 2000) aestivate and then hibernate in mountains. *Coccinella septempunctata* has like behaviour in Greece (Katsoyannos *et al.*, 1997). Similar aggregations of the endomychid beetle *Stenotarsus rotundus* occur during dry seasons in Panama (Wolda and Denlinger, 1984).

During redistribution the numbers completing transfer diminish with distance from the origin, giving rise to a hollow graphic profile (Taylor and Taylor, 1977; Taylor, R.A.J., 1978, 1980; Fig. 10.21). Most individuals fly short distances while a few fly longer ones. This profile often fits a *negative exponential*. But an *inverse power function* fits data on the movement of a population of skipper butterflies better, as it does not truncate the distribution of distances travelled unduly (Hill *et al.*, 1996). Many workers have employed mark/recapture methods to estimate dispersal (Corbet, 1952; Cook *et al.*, 1976; Michiels and Dhondt, 1991). But these often underestimate the distances insects travel since the study areas have often been too small (Franzen and Nilsson, 2007). Unsurprisingly, recent work has often given better estimates (Hanski *et al.*, 1994). See the massive trapping efforts of Guichard *et al.* (2010), covering almost 400 km^2. Also, redistributing insects can die anywhere: within patches, habitats, danger zones, the matrix and beyond their breeding limits (Section **12.3.4.1**).

Redistribution, then, includes *migration and dispersal*, but its evolutionary significance is complex, especially so if long-distance migration has no return. It is the displacement of individuals, who later seek new resources either within the natal habitat or beyond. During redistribution the individual seeks no resource but displaces itself in an undistracted manner. Johnson (1969) gives many examples. It functions to reduce aggregation of relatives (potential competition from kin and inbreeding depression). It may allow individuals to avoid dwindling food supplies, pollution by conspecific individuals (Thompson, 1956), parent–offspring conflict (Trivers, 1974; Hamilton and May, 1977; Taylor, 1988; Starrfelt and Kokko, 2010) and the build-up of enemies. For parents it spreads risk (den Boer, 1968). In the long term it avoids catastrophe. Since it often mixes populations, it recombines genetic material but slows or prevents the evolution of locally adapted races (Haldane, 1956; Slatkin, 1987; Burt, 1995; Mopper *et al.*, 1995).

Insect migration often entails high risk (Harrison, 1980), so if it is safer to stay why do many individuals leave? Are the reasons above sufficient explanation? Milkweed beetles often fly away from suitable food (Davis, 1984), and *Trypoxylon* from ostensibly suitable nesting sites (Freeman, 1981a). In *Melittobia,* the estimated chance of a migrant female finding a new host wasp is 1 in 485 but that for one staying near the host's nest is 1 in 29 (Freeman and Ittyeipe, 1993). What could migrants gain by participating in such mass suicide? *Nilaparvata* (Section **5.3.1.2(d)**) migrating into Japan in autumn (Wada *et al.*, 1987; Kisimoto and Sogawa, 1995) and *Anticarsia* (Section **5.2.1.4(j)**) near their northern limit in the USA have almost zero chance of leaving progeny, the '*pied piper*' problem (Pedgley *et al.*, 1995). Yet the migrations continue. So the question poses difficulties for evolutionary theory (Bell *et al.*, 2005) and the definition of 'fitness' (q.v.). However, increasingly less obvious return migrations are being found (Taylor and Reling, 1986b; Walker, 1991; Johnson, 1995; Chapman *et al.*, 2015). Large-scale return migrations of *Heliothis armigera* occur in northern China (Feng *et al.*, 2005). These moths re-migrate selectively on

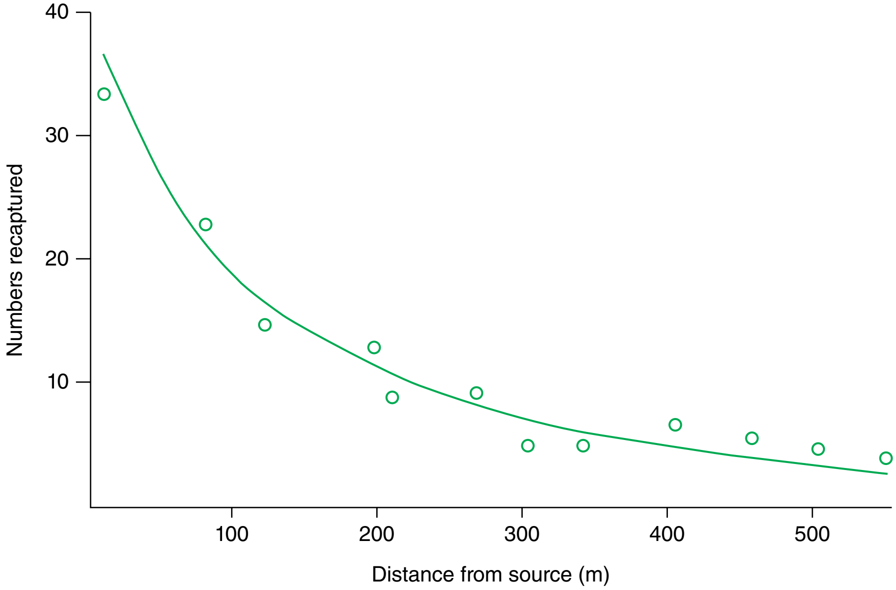


Fig. 10.21. Distances travelled by migrant *Drosophila*. The plot is based on data from Taylor, R.A.J (1978) The relationship between density and distance in dispersing insects. *Ecological Entomology* 3, 63–70. Reproduced with permission.

strong northerly winds, often travelling >600 km per night.

Theoretical evaluations of dispersal in *persistent habitats* are given by Hamilton and May (1977), Comins *et al*. (1980), Comins and Noble (1985) and Motro (1983). One result is that an *evolved reduction of risk* during migration will make it more frequent. This is intuitively reasonable and relates to ISC discussed next. In an inclusive fitness model, P.D. Taylor (1988) takes the very necessary step of including the *chance* a migrant offspring has of finding a new patch. Clearly, this decreases with distance and is covered by the parameter *c*. When *c* = 1 no migrant is successful, when *c* = 0 all of them are. The fraction dispersing becomes greater as *c* nears zero (see Figs 1–3 in Comins and Noble, 1985). A fitness trade-off occurs since those dispersing avoid competition with relatives left behind, so partly offsetting dispersive risk. Omitting the cost of staying put, migratory costs are *twofold* (Stamps *et al*., 2005): (i) risk of death in transit in the landscape (Hanski and Gyllenberg, 1993; Tischendorf and Fahrig, 2000); and (ii) loss of fitness as a result of migration. Mating before migration also affects the fraction leaving. Slatkin (1987) and Drake *et al*. (1995) consider selection on the gene pool of migrants, while Ruxton (1996), in a spatial model, examines the effects of density dependence on the proportion leaving. But when patches have short duration, dispersal is obligatory (Harrison, 1980; Section **12.2.3**).

Then there are species showing flight polymorphism (Section **11.2.3.1**), or like locusts and *Melittobia*, flight polyphenism. Flight ability is dependent on flight equipment. But the balance of redistributive effort, in relation to current conditions, relates not only to the fitness of migrants versus non-migrants, but also to that of their parents (Hamilton, 1996). Migration provides a further case of parent/offspring conflict (Motro, 1983; see also Trivers, 1974). Parents prefer more migrant offspring than do the offspring themselves. If dispersal is under parental control the distances covered would be greater than those preferred by the offspring (Starrfelt and Kokko, 2010). So parental fitness, not only that of offspring, may be the key to unravelling risky migration, another ecological process that needs an evolutionary perspective for a full understanding.

While the strategy of having *environmentally induced* rather than *genetically determined* migratory behaviour in a progeny would seem to cover most contingencies, examples of genetic control of wing polymorphism are well known. They include

Gryllus (Orthoptera; Roff, 1984), some carabid beetles (Roff, 1986), the weevils *Sitona* (Jackson, 1928) and *Apion* (Stein, 1973), and the bugs *Nilaparvata* (Mochida, 1975) and *Oncopeltus* (Dingle, 1968). In the bug *Horvathiolus* (Solbreck, 1986), although a single locus determines brachyptery or macroptery, flight muscle development is environmentally induced. In *N. lugens* macroptery is correlated with melanism, which may have thermal outcomes for flight (Denno and Roderick, 1990). In general, flight polymorphism is polygenic in exopterygotes and monogenic in endopterygotes (Roff, 1994). But not all macropterous morphs fly (Johnson, 1969; Roff, 1990; Zera and Denno, 1997), as in the moth *Malacosoma pluviale* (Wellington, 1957) and the gall midge *Asphondylia* (Freeman and Geoghagen, 1987). Thus, the determination of migratory behaviour, not simply of macroptery, is the point at issue. The strategy of *Melittobia* provides a complex case. Female progenies are determined environmentally by their degree of crowding as larvae to be of three forms, crawlers, jumpers and fliers (Freeman and Ittyeipe, 1982; Sections **8.2.2.1** and **10.2.4.6**). So the distance moved by such offspring is trimodal, instead of the usual bimodal one where there are migrants and non-migrants. Roff (1994) developed models to show the advantage of flight polymorphism in fragmented environments. If there is a single gene for brachyptery it is dominant. Mating must occur before migration, which is common in endopterygotes, otherwise only the allele for macroptery could persist. His single-locus model shows how a gene for brachyptery will spread in a population, the mean proportion of brachypters being related critically to the duration of patches (see Section **12.2.3**). The longer this is the higher their proportion. In the Delphacidae mating occurs after migration, but flight polymorphism is polygenic.

Recall that *appetitive movement* is quite different in scope and function from that of redistribution, being a specific search for favourable patches, resources or mates. It may lead to a *consummatory act* such as feeding, basking, or mating. It often forms part of a daily cycle of activity, but may be seasonal or otherwise periodic, such as the alternation of feeding with reproduction in locusts (Section **5.2.1.1**), cockchafers (Section **3.2.1.2(b)**) and biting flies. It comprises organized sequences of behaviour, termed *behavioural repertoires*. These have been studied, especially diurnal ones, from early times by Jean Henri Fabre (1882), the French father of insect behavioural studies. Tinbergen (1935) and Baerends (1941) for nesting in solitary wasps, Salt (1935) and Vinson (1984, Fig. 2) for searching parasitoids. Dethier and Bodenstein (1958) studied food finding and feeding in the blow fly *Phormia regina*, and showed that the search phases must take place in a fixed, catenary sequence. These involve a series of visual, chemosensory and tactile cues inducing mechanistic responses. When *Phormia's* crop is full inhibiting neural impulses pass to the central nervous system; if the special nerve is cut the fly continues feeding until the distended beast dies! Similarly, abdominal stretch receptors signal a full blood meal in *Aedes aegypti* (Bowen, 1991). There have been thousands of similar studies since then, and of course, these sequences are subject to evolution (Dethier, 1980). A revealing technique is to analyse them by Markovian chains (q.v.) (Hanley, 1984; Root and Kareiva, 1984; Hoffmeister and Gienapp, 2001).

Appetitive movement by *juveniles* occurs mostly within the patch or habitat (Sections **9.5** and **12.2**; Southwood *et al*., 1974). That of *adults* may or may not be so confined. Resources are sought diurnally, such as those for food and shelter, or seasonally, such as those for overwintering sites. This occurs in the weevil *Apion*, (Freeman, 1965) and carabid and Colorado beetles (Hunt and Tan, 2000), but also for aestivation sites (*Heliothis armigera*), or both (ladybirds, e.g. *Semiadalia*; Yakhontov, 1962). Although these may take the individual to an adjacent refuge habitat or farther afield in the landscape, they are essentially appetitive movements.

Indeed, the adults of many species use topographical, often linear features, to assist seeking. Mosquitoes and simuliid flies often select woodland edges, hedges and river banks. Dragonflies follow rivers when feeding. *Papilio homerus* females course along forest streams (Garraway *et al*., 2008) and those of *Celastrina argiolus* (Section **12.2.3.1**) follow hedges when seeking to oviposit. Some swallowtails, nymphalid butterflies and a few tachinid flies fly to hill tops when seeking a mate, a feature improving habitat connectivity (Tscharntke and Brandl, 2004). Male *Sirex noctilio* fly to the top of pine trees where they form a lek, later joined by virgin females seeking a mate (Sarvary *et al*., 2016). Insects such as wasps, bees and territorial butterflies, including several Nymphalidae, learn the anatomy of the locale (Baerends, 1941; von Frisch, 1967/1993; Janzen, 1971; Freeman and Johnston, 1978b; Baker, 1983; Vane-Wright and Ackery, 1984; Dyer, 2002; Reinhard *et al*., 2004). The ichneumon *Hyposoter horticola* has a good spatial memory, visiting its host's egg clusters repeatedly, until they are ready for parasitism (van Nouhuys and Kaartinen, 2008; Section **11.5.2.3**). Learning is not only visual, parasitoids such as *Cotesia* and *Microplitis* learn blends of specific plant volatiles (Hilker and Meiners, 2006).

Following specializations, the normal mobility of some adult pterygotes is reduced (Waage, 1979; Roff, 1990). Earwigs, heteropterans and beetles use their forewings as armour, so impairing their flight function (Wootton, 1992). We note that protective coloration (Section **10.2.3.5**), as in Lepidoptera, has no such negative effects. Adult scale insects are sedentary. The ectoparasitic Mallophaga, Siphonaptera and Siphunculata are flightless, which gives us insights into flight polymorphism (above). Some adults lose their flight ability once they locate reproductive resources (e.g. clover seed weevils, some bugs and carabid beetles), because their flight muscles regress. Post-dispersive termites, ants and Pupipara excise their wings. Although most adult insects can walk, dragonflies do this poorly as their legs are modified for capturing prey and they cannot fold their wide wings.

Escape and resource seeking derive from an idea expressed by the seventeenth century philosopher Thomas Hobbes, that we, like other animals, avoid bad things and seek good things (Russell, 1961): the *appetites* and *aversions* of Craig (1918). Escape occurs according to perceived threat (bad). Appetitive movement, often resource seeking (good), occurs according to physiological state (Kennedy, 1967): physiology drives behaviour. Both involve sensory input. We deal further with escape from enemies in Section **10.2.3.9** and **10.2.4.8**.

Apart from the well-known aspects of movement discussed above, there is a further generality concerning the evolution of flight and resource seeking that needs consideration. It is an axiom that when flight first evolved it would not be very effective (Wootton, 1976). But today in Lepidoptera, Diptera and Hymenoptera, adults in certain families have evolved separately through large size, high-energy turnover relative to this size, a complex neurosensory system and a rapid and precise flight (Kammer and Heinrich, 1978), a quite *exceptional individual capacity* for an invertebrate *to redistribute* and *then to seek and find* scattered resources. Redistributive flight is fast and usually low level (<5 m; Baker, 1968, type 2 above). *Subsequent* resource finding compounds the rate of discovery of each item and the absolute distance between them. I call this ability *individual searching capacity* (ISC, when highly developed HISC, when poorly developed LISC).

The high rate of energy consumption for HISC is sustained by collecting flight fuel rapidly (Kammer and Heinrich, 1978), although the fat body can contain copious energy stores (see below). HISC insects vary in their rate of fuel use, especially because neurogenic fliers are usually less lavish than myogenic ones (Section **1.2**). The time cost of searching is always minimized. The ecological outcomes of HISC have not been described comprehensively before, although Flanders (1953) mentions 'high searching capacity' in parasitoids, and Southwood (1978), with whom I discussed the idea, uses the phrase 'the evolutionary forces for the development of an ability to orientate'. Bennett (1991) considers the evolution of 'activity capacity', but nowhere links it to searching and finding. Heinrich (1977), however, refers to the rate 'at which an animal acquires and expends energy', while Vermeij (1994), after Thompson (1929), argues that RS is limited by an animal's ability to find, consume and perhaps defend resources. Then, a measure of progressive complexity is an increasing richness and variety of behaviours (Szathmáry and Maynard Smith, 1995), which fits the outcome of HISC clearly.

To repeat, I refer to *an individual not a population* capacity like that modelled in Nicholson and Bailey's 'area of discovery' (Dusenbery, 1989; see Section **11.2.2.2**). HISC contrasts the *en masse* migration of aphids and frit flies high in the air, following which few of many individuals locate a new resource. For migrant aphids, 'mortality ... is of the order of hundreds, possibly thousands to one ...' (Taylor, 1977), while for migrant *Rhopalosiphum*, Ward *et al*. (1998) estimated a mere 0.6% success. Locusts are anomalous: they are large, search downwind in swarms, but although speedily covering great distances, have little control over landing because they cannot fly slowly (Wootton, 1992) and often drown in water bodies (Section **5.2.1.1(a)**). Further, in LISC species the post-migratory appetitive phase is repeated on only a small spatial scale, as in *Myzus persicae*. So, while both *r*-selected and HISC species are highly mobile, their migratory modes (Section **12.3.4.4(c)**) and resource finding are distinct. Wind largely determines the path of high-level migrants, less so in low-level ones. So environmental scanning is by myriad, small, LISC offspring (mass migrants, mass scanning), by few, large HISC ones, (individual scanning; q.v.), or, like mosquitoes and simuliid flies, somewhere in between. In addition, *r*-selection for small size and rapid reproduction is incompatible with that for large size and HISC.

Large size is often an outcome of HISC evolution. Prior to resource seeking several big butterflies including *Anteos*, *Hebomoia* (Pieridae) and *Historis* (Nymphalidae) (Dudley, 2000), and some big noctuid and sphingid moths (Janzen, 1984), redistribute over many kilometres, mainly under their own power. Big hawk moths have been seen flying strongly ~100 km off the Queensland coast (D'Abrera, 1986). Females of the Neotropical hawk moth *Amphimoea walkeri* approach 200 mm wingspan (why so big?). *Cocytius anteus* has similar span and weighs >6 g (Bartholomew and Heinrich, 1973, in Casey, 1976). In Finland bigger, strongly flying moths are better colonists of isolated islands (Nieminen and Hanski, 1998). After migration such moths locate many different nectar sources and distribute eggs on several widely spaced, specific food plants (Janzen, 1984). The ability to find and orientate rapidly to many discrete resources, such as flowers for feeding or carcasses for oviposition, is the epitome of HISC. While a hawk moth, using precise flight control (Sane *et al*., 2007; Wang, H., *et al*., 2008), visits dozens of resource items in a night (below), locusts and some aphids merely crash land (see above and Section **5.2.1.1(d)**; Kring, 1972). In such moths wing-beat frequency, amplitude and attack angle are controlled precisely, and the smaller ones (*Macroglossum* spp.) have the highest wing-beat frequency (50–80 Hz) of any insect with synchronous flight muscles (Section **1.2**; Casey, 1976; Marden, 2000). They are 'high-performance' insects (O'Brien, 1999). Improving ISC promotes increasing divergence from random search. Similarly, big Diptera in the Tabanidae, Syrphidae and Cyclorrhapha locate individually multiple, widely spaced food and reproductive resources with speed. Of the Tabanidae, Colyer and Hammond (1951), vastly experienced field entomologists, note that they include 'some of the largest and most rapidly-flying' British Diptera. Since HISC can be employed in dispersive or congregative behaviours, we expect these insects to have sparse (*Tabanus*, hawk moths) or locally dense (social Aculeata, blow flies) populations. Long ago in a Hertfordshire woodland, I was gutting a rabbit my brother-in-law had just shot; before we could bury the hot entrails a score of blow flies had found them, such is their power of searching and finding. Burying beetles locate carcasses in hours (Scott, 1998), but they use only one resource item for ~2 weeks. Finally, HISC insects never show full alary dimorphism (Zera and Denno, 1997; Sections **11.2.3.1** and **12.3.4.1**) and while individuals naturally vary in flight capacity, they usually improve as they mature (Marden *et al*., 1998). Impressively, some libellulid dragonflies double their mass, mainly as the result of increased thoracic musculature, during the first 2 weeks of adult life.

After migration, HISC insects find and use multiple, widely scattered *specific resources* (plant or animal), an ability comparable with that of passerine birds, although the latter are less affected by inclement weather (Hinton, 1973). It has outcomes not only for redistribution but also for finding resources. HISC has widespread effects on life-history strategies, population dynamics and genetics, especially in metapopulations (Harrison and Hastings, 1996). Here, small groups are isolated only when juvenile, while little adjacent patches in habitats for LISC insects compare with widely separated ones in landscapes for HISC insects. Migration aside, LISC insects often inhabit fine-grained environments, HISC insects course-grained ones. They apply their capabilities to diverse lifestyles. For example, dragonflies, asilid flies and aculeate wasps are formidable predators (Section **8.2.2.4**), calliphorid flies carrion feeders, first to arrive on the scene, euglossine bees the ultimate pollinators, and tabanid flies out-fly their running ungulate prey. And they easily avoid avian predation (Marden, 1987). In all, extreme physiological/behavioural developments, such as HISC, offer up new ecological possibilities.

Thus, aculeate Hymenoptera provide a special case of the diverse applications of ISC. While most HISC insects use multiple patches, wasps and bees, both solitary and social, have developed the characteristic out-and-home flight pattern from nest site to food sources (Tinbergen, 1935; von Frisch, 1967/1993; Michener, 1974), they are *central place foragers*. Honey bees, having learnt the environs of the nest site, recognize quite specific features of local scenery, using them as landmarks on their return (Dyer *et al*., 2008). On arrival they compare the brain's stored image of the nest site with that observed, until a match is found (Collett, 1996), called *image matching*. In addition, in solitary species there may be a localized night roosting site (Linsley, 1962; Freeman and Johnston, 1978a and b; Rosenheim, 1987). *Sceliphron assimile* when building and provisioning cells uses several different paths from mud source to nest, alternating between them and so probably reducing the risk of avian predation. In large euglossine bees (Dressler, 1982), HISC is extreme and flight very rapid. Trips from the nest cover many kilometres. Janzen (1971) recorded a marked *Euplusia* returning to her nest from 20 km in 65 minutes, having collected a full load of pollen! Their flight muscles are the most active tissue known (Heinrich, 1993). Indeed, the pollination syndrome (Section **8.2.1**) may be a driver of ISC in bees and butterflies. Learning the landscape is common in Hymenoptera. In bees its spatial scale increases with size and increasing ISC (Raw, 1985; Guédot *et al.*, 2009). The distance between the wing bases (intertegular span) is a good measure of size here. It relates not only to thoracic size but also to dry body mass (Cane, 1987, in Greenleaf *et al.*, 2007) and is directly related to flight speed in *Papilio machaon* (Dempster *et al.*, 1976; below).

Many dragonflies, alone in the exopterygotes, have HISC. Some have feeding and breeding areas many kilometres apart (Corbet, 1999; Macagno *et al.*, 2008; Section **8.2.2.3(a)**). Their flight ability is also crucial when males defend territories. But some dragonflies (and big butterflies) with their lower wing loadings, often glide as well as fly strongly, so conserving fuel (Kammer and Heinrich, 1978). Surprisingly, they also have low drag coefficients (<0.5) (Willmott and Ellington, 1997), as well as high speed and great acceleration (May, 1991; Marden, 2000).

Our suspicions that something fundamental is happening in such insects are aroused by comparing their MR with those of birds during resting and flight. As expected (Section **10.2.2.2**), in both groups resting metabolism declines with body mass (BM). MR also declines with BM in flying birds, but does not always do so in flying insects: there is great variation. Big hawk moths like *Manduca* are of similar BM to locusts, but mass-specific power output of hawk moth muscle is ~2.5 times greater, while that of *Bombus* and big Cyclorrhapha is more than five times greater (Kammer and Heinrich, 1978). The mass-specific O_2 consumption in *Manduca* is about five times that of locusts (Harrison and Roberts, 2000). Remarkably, and going against the general trend (Casey *et al.*, 1985), in two euglossines *Euglossa dissimula* (91 mg) and *Eulaema meriana* (820 mg), the muscle mass-specific power under experiment is greater in the heavier bee (90 W/kg and 110 W/kg; Dudley, 1995). This result partly obscures the BM/MR relationship in flying insects, but is no surprise under the rationale of ISC. Bees and wasps need extra power for carrying materials and in euglossines thoracic muscle mass is ~30% of BM. Aerodynamic profile is rarely discussed. But the drag coefficient of *Bombus* workers is 0.63, rather less in honey bees and in *Manduca* is only 0.25–0.30, the smooth covering of scales likely promoting such efficiency by reducing the 'parasite power' requirement, which is proportional to the cube of flight speed (Harrison and Roberts, 2000). In contrast, the drag coefficient in locusts is ~1.47 (Willmott and Ellington, 1997). Small insects, with their greater surface area to body mass, suffer relatively greater drag in flight. Flying dung beetles appear grossly encumbered, but related bumble-flower beetles (*Euphoria*) have a smooth surface, close their wing cases in flight, fly much faster and visit many flowers.

Insect flight is far different from that of fixed-wing aircraft as insect wings provide both propulsion and lift. Rayner (1979) proposed a model of animal flight in which a series of vortices are flung into the wake of the flight path, but this produces inadequate lift. Later, a *leading-edge vortex* was discovered (below) and found to improve performance. But power without control has little value. Insects, like fighter planes but unlike airliners (Dunt, personal communication), are unstable in flight (Ellington, 1995; Usherwood and Ellington, 2002), having 'unsteady dynamics', and adjust roll, pitch and yaw rapidly as they fly (Sane *et al.*, 2007; Taylor and Krapp, 2008). Control is achieved using constant inputs from four sensory organ systems: (i) visual sensors (compound eyes, ocelli); (ii) airflow sensors (antennae, wind-sensitive hairs); (iii) inertial sensors (halteres and others); and (iv) wing-load sensors (campaniform sensilla). It becomes clear in reading these papers that the insects already designated as HISC (big bees, blow flies) are equipped with more elaborate flight control systems than LISC insects (roaches, locusts). Compound eyes provide key sensory input for flight control. Unsurprisingly, HISC insects have thousands of eye facets. Blow flies have ~6000 ommatidia in each eye.

Retinal image flow is fastest when flight is close to objects, slowest when far away. Using this principle, bumble bees fly fast in the open and slow near objects (Baird *et al*., 2005). The visual neuropiles, in which retinal information is analysed, are more complex in *Calliphora* than in *Drosophila*. The antennae and Johnston's organ (a proprioceptor) are elaborate in big calypterate flies. They also have many (~335) sensilla on their halteres (Chan *et al*., 1998). *Calliphora* uses inputs from these organs via the visual inter-neurones to adjust flight rapidly (<30 ms). They are extremely agile, partly due to a complex wing structure (Wootton, 1992), and show rapid anemotaxis to specific ecomones, their antennae having a diversity of sense organs (Gewecke, 1974, in Kammer and Heinrich, 1978; Wigglesworth, 1984). Dragonflies use their big heads as inertial detectors, using proprioceptors in the neck to record angular acceleration. But no advantage lies in having complex sensory input unless the central neural processing is adequate to analyse it and the motor system sufficient to respond to it. Indeed, blow flies have a large, condensed thoracic ganglion, perhaps speeding up flight control.

There is a dichotomy in resource-seeking behaviour relating to the duration and type of flight, and in turn to the type of fuel insects burn. Myogenic fliers in the Diptera (Roff, 1977) like parasitic flies, and Apocrita, burn sugar, fly relatively fast, and have high wing loading and beat frequency (Dudley, 2000; Sections **13.2.4.6** and **13.2.4.7**). They must refuel while searching and find scattered nectar sources quickly. The fuel obtained must match that used in flight and maintaining muscle (Zera and Denno, 1997). Hovering while feeding, as in hawk moths, while lavish on fuel permits detailed perception of a potential resource and speeds up its collection (Kammer and Heinrich, 1978). Here the stroke plane of the wings is near horizontal (Sun and Xiong, 2005), while in hawk moths at least, a vortex develops along the leading edge of the wing greatly improving lift (Liu *et al*., 1998). Some insects use anaerobic metabolism at such times of peak power consumption (Harrison and Roberts, 2000). Fat burners, like locusts, beetles and some Lepidoptera, usually fly more slowly, have neurogenic flight and a relatively low wing-beat. So they should be capable of longer searching periods between refuelling.

The physiology of flight fuel use is complex. Sugar burners metabolize the disaccharide trehalose in their muscles, while fat burners use triglycerides. Then there are a few odd cases: some scarabaeid beetles, Colorado beetles and tsetse use the amino acid proline. Locusts switch from carbohydrate to lipid fuel after ~30 minutes of flight, desiccation being offset by metabolic water production further extending flight duration. Desert locusts have crossed the Atlantic (Skaf *et al*., 1990), albeit a minuscule fraction of those leaving the Sahara. Hawk moths, after a brief start-up on sugars, may also use lipids (Ziegler and Schulz, 1986b; Joos, 1987), but O'Brien (1999) found for *Amphion*, that they burnt them only when short of nectar. The fat body is a capacious store of energy and other resources (Ziegler and Schulz, 1986a and b). Blow flies and wasps (Casas *et al*., 2003) always fuel their flight muscles with carbohydrate. Excess nectar, however, is stored as fat, which no doubt relates to its greater energy content per unit mass (by a factor of about eight) than carbohydrate (Kennedy, 1961b; Dudley, 2000). But many insects maintain carbohydrate stores too: there is much variation in flight fuels within insect orders. As usual, things are less simple than they first appear. Furthermore, many workers on insect flight physiology, but not J.H. Marden and R. Dudley, fail to address the differences between migratory and appetitive phases of insect behaviour.

As in other life-history tactics, ISC involves co-adapted traits (Section **9.1**).

1. Large body size evolves. Small insects fly weakly and are prey to even light winds (Lewis and Taylor, 1967). In theory, flight speed scales at $m^{0.17}$ of body mass (m) (Dudley, 2001) and observed maxima range from 0.5–10 m/s. But life cycle in large insects cannot be short (Danks, 2006). Several adult euglossines are long lived, averaging 91 days in the big *Eulaema meriana* in captivity, while a few wild *Euglossa imperialis* were recaptured after 56 days (Ackerman and Montalvo, 1985).

2. Following this an efficient, energetic flight motor evolves (Vermeij, 1994; Dudley, 2001), involving heterothermy (Heinrich, 1993; Section **10.2.4.2**). Large size permits effective thoracic insulation and heat conservation, impossible in a gnat-sized insect. Thoracic scales in hawk moths allow fast warm-up (when they are vulnerable), but also reduce drag (above). Cooling in flight, as in *Bombus*, is via the poorly insulated abdomen, and wings.

3. A sensory system scanning distances of many metres and a central nervous system capable of processing such enhanced information evolve. Large eyes with small inter-ommatidial angles maximize visual acuity (Land, 1997) and assist in assessing self-motion (Baird *et al*., 2005).

While large body size is an essential, miniaturization of the neural system may be at work. These biofacies conform to four discussed by McShea (1998) to explain major evolutionary trends, namely energy intensiveness, size, complexity and adaptedness, although the last-named is a difficult concept (Gould and Lewontin, 1979). Apart from ISC evolution in insects, a similar progression has occurred in cephalopods, from *Nautilus* to squids (Vermeij, 1994).

So, HISC insects are complex and as Fisher (1930) first pointed out and Endler and McLellan (1988) and Orr (2000) have discussed lately, complexity bears evolutionary costs. A mutation is less likely to be favourable in a complex than in a simple organism. Orr suggests that complex organisms may have greater difficulty in adapting to changing environments (all organisms play perpetual evolutionary catch-up; Section **9.7**). But while the problem remains in evolutionary time, HISC insects can select *currently favourable* places for reproduction, so spreading risk widely for the progeny. Their very complexity permits better *present* adaptation. Wide-ranging species, evolving in relation to a variety of habitats, should develop great genetic diversity (Habel and Schmitt, 2009). As expected, they are not tenacious or specific to a habitat. Many travel the matrix (Ricketts, 2001), and eggs are laid on widespread suitable resource patches wherever they are found. Then, while growth to large size and the development of complex structure are incompatible with an *r*-strategy, the *relative* energetic costs of flight decrease with increasing body size (Harrison and Roberts, 2000). Apart from moths, HISC insects are diurnal and may discriminate pattern and colour in finding resources from afar (Section **10.2.4.4**).

Flight speed is critical for another reason in that it allows better control when windy. Even within a species speed is a size-related variable. In *Papilio machaon* males with the widest thoraces fly faster (2.7 m/s) than those with the narrowest ones (1.5 m/s) (Dempster *et al*., 1976; above). Size effects behaviour in confamilial species. *Nathalis* and *Eurema* spp. (Pieridae) are small and flutter slowly near the ground, *Ascia* and *Pieris* are rather larger, fly rather faster and higher, while *Anteos merula* and some Asian *Hebomoia* are large and fly swiftly at heights of several metres. Most little lycaenid butterflies (not hairstreaks) are confined to low plants. By contrast *Historis odius* (Nymphalidae), a large, robust Neotropical species, and magnificent *Morpho* spp. patrol forests at heights of 5–10 m or more. Wind speeds are typically faster high above the ground (Section **10.2.4.5**), but diurnal insects capable of negotiating such levels will search broader paths at greater rates (Stanton, 1982, in Turchin, 1998). Even on the ground, big carabid beetles have a greater ambit of activity than small ones do (den Boer, 1998). Small *Calathus melanocephalus* use an area of ~2 ha, medium-sized *Pterostichus versicolor* occupy ~12 ha, but large *Carabus cancellatus* roam throughout ~700 ha (van Dijk and den Boer, 1992). With a few exceptions, however, like big African dung beetles (Bartholomew and Heinrich, 1978), flying bumble-flower beetles (above) and tiger beetles in the sun, Coleoptera do not have elevated thoracic temperatures.

There are further genetic imperatives. Following early work on ecological genetics by Ford and Dobzhansky (Section **11.2.3.1**), Watt (1992, 2000) and Watt *et al*. (2003) made searching studies on flight polymorphism in *Colias* (Pieridae), finding their *Pgi* genotypes coded for polymorphism. There are marked differences in phospho-glucose isomerase, an enzyme critical in the supply of flight fuel. This variation determines flight capacity, thermal relations, mating success in males and egg distribution and hence AF in females. Since in *Colias* adaptation to very *variable* temperature limits the flight motor's performance this should be kept in mind when considering HISC, insects with the greatest flight performance tend to be tropical where temperature variation is least. Again in *Colias*, those with the greatest resistance to high insolation have the least AF, there being a trade-off in fitness components. Haag *et al*. (2005) found that several *Pgi* alleles determine the MR of the flight motor in *Melitaea cinxia* (Nymphalidae). This relates to distribution, but the genotype conferring a high MR in this species (*Pgi-f*) also promotes higher AF and is more frequent in new isolates. Ostensibly there is no trade-off. So in the context of ISC, genetic variation must again be borne in mind.

10.2.4.2 Movement: Physical factors: Temperature and insolation

Since temperature controls MR in most insects, it usually controls the capacity for, and rate of, movement. But it is the *internal* temperature (T_b) in the thorax of adults where the locomotory muscles reside (Section **1.5**), which is relevant. The excess of T_b over ambient (T_a) is trivial in small and/or lethargic adults, but great in large, active ones. The latter adjust T_b well above T_a, either by producing metabolic heat (*endothermic insects*) or by absorbing heat from their surroundings (*ectothermic insects*). Some combine both strategies (May, 1979). Flying hawk moths (*Manduca*), big bees (*Bombus* and *Eulaema*) and big flies (*Tabanus sudeticus*) regulate their thoracic T_b at levels *much* higher than T_a (Heinrich, 1981, 1993). Flying desert bees, *Centris pallida*, regulate such temperature at 45 ± 2°C (Roberts *et al*., 1998) and metabolic heat production can be varied. A T_b of 46°C is recorded in *Manduca* and 38–45°C in the dragonfly *Libellula*. These insects have high ISC (Section **10.2.4.1**), a physiology untenable if they did not find flight fuel quickly. The high T_b in *Bombus* queens permits foraging in late winter. Their thoracic T_b is then ~40°C while T_a may be close to zero. In the moth *Eupsilia* and related genera, an elevated T_b coupled with a heavily insulated (furry) head and thorax, enable them to fly and oviposit early in the year at near zero T_a. But they cannot maintain a high T_b for long when flying and stop periodically and shiver to regain it, using fat stores in the process. Similar shivering occurs in honey bees and worker bumble bees foraging in cool weather (May, 1979). So, with endothermic physiology some insects extend not only their spatial ambit of operations but also their temporal one.

Insects that stay active and exposed during the heat of the day often employ metallic blue, green or gold structural colours to mitigate the effects of high insolation and over-heating (Willmer, 1982). These colours occur in a few dragonflies (*Stomatochlora metallica*), in several endopterygote orders including Coleoptera (Scarabaeidae, Chrysomelidae), Diptera (Syrphidae, Dolichopodidae, Calliphoridae), even a few mosquitoes (Section **7.3.2.4(c)**), and in Hymenoptera (some Parasitica and bees). Metallic carabid beetles occur in sunny places, black ones in shade (Szujecki, 1987). Evaporation allows cooling, but some endothermic insects reduce wing-beat frequency and metabolic heat production in hot conditions (above; Harrison and Roberts, 2000).

Small, weakly flying migrants cannot control their T_b, their activity is entirely dependent on T_a (Kammer and Heinrich, 1978). In *Aphis fabae* different T_a thresholds exist for take-off (17.3°C), upward flight (15.0°C) and level flight (13.0°C), variation being due to different energetic demands for these activities (Taylor, 1963). But medium-to large-insects can elevate their T_b above ambient by basking. Movement allows them to reduce the deleterious effects and maximize the beneficial effects of microclimatic variation. On dull days most insects do not fly at all. Under temperate conditions especially, the duration of sunshine has critical outcomes for adult movement and other dependent attributes, like AF (Turner, J.R.G. *et al*, 1987). Thus, a cold spring reduces the AF of *Anthocharis* (Section **10.1.2**), while in *Carcelia gnava* (Tachinidae) searching for its larval host *Bupalus pinarius* in the field (Section **11.3.1**), the hours of sunshine determine efficiency (Klomp, 1959).

As with moisture preferences (Section **10.2.4.3**) insects often have preferences for certain T_a. In such work, however, one must carefully separate temperature and moisture effects. Normally, there is a distinct temperature preferendum, for young nymphs of *Chortoicetes* this is 42°C (Clark, 1947). Strangely, three distinct preferenda exist in *Microplectron* (Chalcidae) (Wilkes, 1942, in Andrewartha and Birch, 1954). In a range of experimental temperatures most wasps preferred 25°C, but others preferred 15°C or 8°C.

10.2.4.3 Movement: Physical factors: Precipitation and moisture

Insects seeking favourable microclimates may show any of three simple behaviours that are most easily studied when they walk.

1. In *orthokinesis* they move rapidly in harsh conditions such as dry air and slowly in favourable humid ones.
2. In *klinokinesis* the frequency of turning movements increases, which occurs once a resource has been located, and/or serves to limit penetration into an unfavourable (dry) zone. As long as the reaction is immediate, *move length* will be less in the harsh zone.
3. *Klinotaxis* is a direct recoil, hence *–taxis*, from the harsh zone. This behaviour is found in bush crickets at the boundary of their preferred habitat (Kindvall, 1996, in Turchin, 1998), and by *Agriotes* larvae. But klinotaxis is relatively infrequent.

On a greater spatial scale, fast-flying insects in an appetitive phase often move up-wind when they sense high humidity, pheromones from potential mates, or kairomones from food plants (Section **10.2.4.1**).

This is called *anemotaxis*. Two physical factors, humidity and wind, act together. But as with low temperature, rainfall usually inhibits flight, for example in butterflies, cabbage root flies (Finch and Skinner, 1975) and generally terminates migration (Gatehouse, 1997). On the other hand, the high humidity following substantial rainfall induces dispersive flight in many termite and ant reproductives.

10.2.4.4 Movement: Physical factors: Light and colour

Recall the differences between incident and reflected light (Section **10.2.3.5**). The photoperiod of the former permits or does not permit movement, most insects being either diurnal or nocturnal. Moths attracted to streetlights at night soon become inactive, illumination suppressing flight. Although light in any form does not enter into an insect's physiology to influence movement in the way temperature and humidity may do, the pattern of light, both incident and reflected, is influential as it permits insects to orientate diversely. While diurnal insects see colours at specific peaks (Briscoe and Chittka, 2001; Kelber, 2001; Section **10.1.1**), nocturnal ones, excepting hawk moths (Section **10.2.4.1**), are better at detecting contrast and often movement at low illuminance (Allan *et al*., 1987).

The spectral peaks that most diurnal insects see are shifted towards shorter wavelengths than we see. They respond to ultraviolet but rarely to red (Hinton, 1973; Prokopy and Owens, 1983; Briscoe and Chittka, 2001). Visual information, however, is conditioned by the light environment in which it is perceived ('sight and hearing are inaccurate witnesses'; Sections **10.1.1** and **11.5.1**). Plants have evolved to respond to insect vision. They employ red, anthocyanin pigments when the attention of insects is not to their advantage. Thus, the young shoots and leaves of several trees (mango, maple) are red. Others (beech, plum) have varieties with all-red leaves. *Hoplocampa* prefer to lay eggs on white rather than on pink flowers (Section **6.3.1.1(f)**) and small white butterflies do not oviposit on red cabbages. While yellowing, autumnal leaves of some trees are attractive to specific aphids (Holopainen and Peltonen, 2002), others are rarely found on red leaves (Furuta, 1986; Döring *et al*., 2009). The autumnal synthesis of red pigment *masks* the yellow due to omnipresent carotenoids. While aphids have no red receptors, they can distinguish red from green (Döring *et al*., 2009). These anthocyanins are specially produced (Archetti *et al*., 2008) and associated with phenolics (Section **2.4.2**). But apart from being unattractive to most insects, red pigments in leaves may protect these organs from biochemical imbalance at low temperature. So the redness of young shoots may function differently in tropical and temperate regions.

But autumnal leaf colours are still much of a mystery: why do many poplars have bright yellow falling leaves while those of ash (*Fraxinus*) usually remain dull green? Why do tropical mahoe trees retain a few bright yellow leaves although they are not deciduous? Indeed, there is a wide variety of colours in tree leaves. Then, the yellowish/green hues of young shoots, as in citrus, attract many herbivorous insects. Foliage colours usually lie between 500–580 nm, which insects can probably distinguish in contrast to wavelengths outside this range. Thus, reflectance from dead leaves, bark and soil is usually >580 nm, although some fallen leaves and flowers retain their colour. Some butterflies can distinguish leaf shape, while host shape recognition is part of the selection process in some parasitoids (Cooperband and Vinson, 2000). Of course, floral colours have co-evolved with insect vision (Hinton, 1973; Section **8.2.1.1**). Daytime pollinators are attracted to several colours, especially yellow and blue. Flowers pollinated specifically by night-flying moths are glossy white, reflecting maximum light. So plant colours, via reflected light, influence the appetitive movement of insects diversely.

Diurnal biting flies use colour vision for seeking prey (Allan *et al*., 1987). *Simulium*, mosquitoes and tsetse are attracted to dark blue and red, a fact used in trap design (Section **7.3.2.4(m)**). Solid objects, contrasting with the background, are also attractive. Tsetse and tabanid flies respond to moving objects. So, light affects insect movement in ways other than pattern and colour. *Choristoneura* larvae (Section **5.2.1.4(c)**) are repelled by direct sunlight and move towards diffuse light. They avoid exposure and hide in the foliage they feed on (Wellington, 1948). Light acts not for some intrinsic property, as temperature or humidity might, but for something else, here food. Light acting thus is called a '*token stimulus*' (Andrewartha and Birch, 1954; Leather *et al*., 1993). High light intensity acts as a token for thermal radiation.

Most aphids do not take-off unless well illuminated. While several pierid and some satyrid species are exceptional, most butterflies fly only in sunshine (Endler, 1992), even in the tropics. This suggests that illumination, not just temperature, is crucial for flight, possibly because it allows more cost-effective searching and the avoidance of avian predators (Marden and Chai, 1991). However, insectan visual sensitivity may improve with increasing temperature (Duruz and Baumann, 1968, in May, 1979). Then, more moths are caught at light traps when there is no moonlight. Conversely, some mosquitoes are captured more frequently during full moon, when in effect there is crepuscular light intensity. But an insect's reactions to light frequently change with its physiological state (Section **9.2**) and/or with T_a. Thus, the tsetse *Glossina morsitans* reverses its positive phototaxis when desiccated or at high temperature (~32°C), a reaction taking it away from habitats with high evaporative rates into cooler, damper places among trees. Again, light acts as a token for something else. As we noted before, dark places tend to be humid and illuminated ones dry.

Some insects respond to polarized light, generally by means of their ocelli. The pattern of polarized light in the sky varies with the sun's position, polarization being greatest at 90° to incident light. Also, the plane in which light is polarized varies systematically. Honey bees use these patterns in seeking food and in returning to the hive (von Frisch, 1967/1973; Dyer, 2002). Orientation in relation to the sun is termed *heliotaxis*. In addition, bees judge distance by integrating the motion of objects passing them (Srinivasan *et al*., 2000), the *retinal image flow* (Esch *et al*., 2001). Spatial information is then passed to other workers in the hive by means of special 'waggle dances', a classic case of symbolic communication. Aristotle described these activities, appending the name of a particularly evocative dance then popular in certain parts of Athens. The bee's dance does indeed improve searching (Sherman and Visscher, 2002), although experienced foragers rely largely on their acquired knowledge of local landmarks (*pharotaxis*) (Grüter and Farina, 2008; Grüter *et al*., 2008). The elaborate dance is used merely to stir other workers into productive activity and give naïve ones spatial information. Plant scents carried by returning bees also help in finding the food source (Reinhard *et al*., 2004). Following von Frisch, locusts and many Endopterygota were found to respond to polarized light. The social bees *Bombus* and *Trigona* pass information in their nests about the *presence* of forage by their excited activity and by plant odours, but give no *directional* information (Michener, 1974; Dornhaus and Chittka, 1999).

10.2.4.5 Movement: Physical factors: Mechanical factors

Mechanical factors, involving wind or water, according to their strength can assist or hinder insect movement as well as survival (Section **10.2.3.6**). While locomotion is an innate attribute, movement of the medium in which the insect exists is an environmental factor, but both form components of insect displacement. This is seen clearly in the relationships between wind and flight, where the resultant affects both speed and direction. But movement entails risk (Freeman, 1976; Slatkin, 1987; Lima, 1998) and in extremes significant mortality ensues.

Air masses move from regions of high atmospheric pressure to those where it is low, the *convergence zone*. The only place for this air to go is upwards. As it rises it cools and if it is sufficiently moist, rain falls (Section **2.2.2.2**). This basic meteorology is, for ecology, an interaction between a mechanical factor, temperature and moisture. When an advective wind is blowing, its speed increases with height, an effect that can be described in a *wind profile*. Hence, wind-powered turbines are placed high up. Vegetation and other obstacles exert a frictional drag on moving air that is greatest near the ground. When air speed equals flight speed an individual has reached its *boundary layer* (Taylor, L.R., 1974). Thus, insects flying against or across a moderate wind do so near the ground, and bees, wasps, butterflies and blow flies are often seen to do this. But several Lepidoptera, especially moths, also migrate high in the air, often using fast-moving air masses (Fitt, 1989; Pedgley *et al*., 1995; Gatehouse, 1997; Chapman *et al*., 2002; Stefanescu *et al*., 2007). The processes of atmospheric circulation (Section **2.2.2.1**) are therefore critical aspects of the favourability or otherwise of winds for insect transport (Johnson, 1995; Burt and Pedgley, 1997) and the distances they may cover, the nature of the matrix being irrelevant. Thus, springtime migrations of homopteroids and moths in the Mississippi Basin and in East Asia take place on tropical air and cover great distances rapidly. Return flights in autumn on cool northern air flows, should they occur (Section **10.2.4.1**), are often slower and iterative.

Some low-flying insects monitor the rate at which patterns pass beneath them, using their lower eye facets (the *optomotor reaction*; Kennedy, 1951) and so assess ground speed. These facets are sensitive to wavelengths >500 nm, assisting control input (Prokopy and Owens, 1983). If insects are blown backwards, the reaction becomes negative and they settle. It is also used to assess wind direction by monitoring lateral drift of the observed pattern (below). Due to motion parallax, patterns appear to pass more rapidly the nearer an insect is to the ground, providing further information. In many species the degree of antennal deflection detected by Johnston's organ (Richards and Davies, 1988) allows assessment of air movement, direction and speed.

Light winds assist searching insects to find and follow olfactory cues from mates and resources, because the attractive aerial plumes are elongated and anemotaxis more effective (Lewis and Macaulay, 1976; Dusenbery, 1989). Strong winds, especially nocturnal ones at several hundred metres altitude, permit the rapid displacement found in long-distance migration (Drake *et al.*, 1995; Burt and Pedgley, 1997). But the vagaries of winds relative to the invariant influence of topography produce complex distributions of such migrants in the air and in their deposition on the ground (Pedgley, 1990). *Nilaparvata* often land *en masse* (Kisimoto and Sogawa, 1995). In the Orkney Isles, UK, topography may influence the distribution of winter moth larvae by wind (Leggett *et al.*, 2011). Such effects are associated with coastal winds, mountain winds such as drainage flows down valleys and barrier winds, and accelerated winds through gaps. It is possible that south-east trade winds in Jamaica influence the level of parasitism by *Melittobia* on *Sceliphron* and other solitary wasps, this being higher to the north-west of the island (Freeman, 1974, 1977). In Fujian, China, mountains (Xianxia Ling) limit the northward movement of the citrus psyllid (Fan *et al.*, 2003, in Yang *et al.*, 2006). Outflows of cool, descending air from thunderstorms influence local wind patterns. Large plants also engineer local winds, insects often collect in the lee of hedges, a further case of organic localization (Sections **9.8** and **10.1.2**). But insects rarely fly in strong winds (Cappuccino and Kareiva, 1985). These inhibit take-off and flight of many homopteroids, while those >2.5 m/s even interfere with pollinating flights by powerful hawk moths (Eisikowich and Galil, 1971). Blustery winds make nest provisioning difficult for solitary wasps.

We noted in Section **10.2.4.1** that small, mass migrants such as aphids, move prodigious distances in upper air movements. The minute encyrtid wasp, *Apoanagyrus lopezi*, introduced into Nigeria early in the 1980s to control cassava mealy bugs (Sections **4.3.7** and **13.2.4.6**) had by 1986 reached 16 African countries. This spread probably occurred by wind-assisted flight, although further introductions and transport of infested plants helped. In the USA, flights of several kilometres in the minuscule mymarid parasitoid, *Anagrus epos*, take place annually from overwintering sites on riverbanks into central areas of Californian vineyards (Doutt and Nakata, 1973). Two European *Drosophila* spp. in 10 years spread from British Columbia, Canada, to northern California (Slatkin, 1987). The massive wind-assisted migrations into southern England from France, as in *Pieris brassicae* and *Vanessa cardui*, often occur at low levels when warm, moderate south-east winds prevail. But crosswind and against-wind flights are also known. Locust migrations are generally downwind (Rainey, 1951, 1989; Draper, 1980; Pedgley *et al.*,1995) and are often associated with the Inter-Tropical Convergence Zone (Sections **2.2.2.1** and **5.2.1.1(a)**), which is comprised of ascending winds that bring heavy rains and in train the desert flowering.

Berland (1935), Felt (1937), Glick (1939) and Freeman (1945) made early studies on insects flying high in the air. Berland collected flies and homopteroids higher (>2000 m) than Hymenoptera and Coleoptera (~1000 m); later workers were astounded to find insects as high as 4000 m. Then, C.B. Williams, C.G. Johnson, L.R. Taylor and their co-workers at Rothamsted, UK, published numerous studies on migrant pests (Taylor, 1986). When temperatures exceed a take-off threshold (Section **10.2.4.2**), migrant aphids and many other small insects are attracted to the bright light of clouds and are transported in them and in low-level jet streams. Nocturnal and dawn migrations are associated with temperature inversions (i.e. temperature *increases* with height; Reynolds *et al.*, 2005) and may move at 80–120 km/h (Johnson, 1969; Pedgley *et al.*, 1995; Burt and Pedgley, 1997). Dawn layers often occur in warm strata (see Fig. 8a in Reynolds *et al.*, 2008). Diurnal aphid migrants stop when air temperatures are too low: they shut their wings and fall at a rate of 1–2 m/s, descending from all but the highest levels in <1 hour. So the distance displaced is limited to that of the air mass when its temperature is above a species-specific threshold, but it can be several hundred kilometres. If it is warm enough they may continue to fly at night. Note these interactions between flight (a behaviour) and temperature and wind speed (physical factors).

In South-East Asia, the Afro-European region, Australia and North America, spring winds often blow polewards as warm fronts bring in rain. In late summer cold fronts often blow towards the Equator. Some insects have evolved migratory downwind flight, colonizing higher latitudes where benign summer conditions are expected, maybe to return later (Drake and Gatehouse, 1995). Migrants include pest moths (*Heliothis*, *Spodoptera*, *Anticarsia, Plutella*), butterflies (*Pieris, Vanessa*), even small plant bugs (*Empoasca*, *Macrosteles*, *Nilaparvata*) (Riley *et al*., 1991). Southbound autumn migrations of syrphine flies are recorded from the Swiss Alps (Schneider, 1969). Movements of locusts and grasshoppers occur from and within the Afro-Asian, Australian and the South American deserts (Section **5.2.1.1(a)**), bringing them to new food. While these migrations entail great losses, these must be compared to those that would result from staying put (Section **12.3.3.2**).

Young larvae of moths such as the winter moth, whose females are flightless, may redistribute on the wind on silken threads (Section **5.2.1.4**). Bagworm moths (Psychidae) are an extreme example. Only adult males fly; females are cocoon-bound and merely oviposit on its surface. In a Jamaican *Oeketicus* sp., mature female but not male larvae ascend the tall, slim juniper trees they attack (Freeman, unpublished data), a habit having two outcomes: (i) the elevated position of the females allows wide distribution of their mating pheromone by the wind; and (ii) when the larvae hatch this should increase their ambit of dispersal on silk. In the bagworm *Luffia* (Section **12.3.4.3**), the pupation sites are higher in the trees than the feeding sites (McDonogh, 1939), but he describes no sexual difference. Such movements are classified as pre-ballooning behaviour (Bell *et al*., 2005).

While many resources are sought using vision and olfaction within habitats, appetitive movement by flight on landscape scales is often downwind, and so faster and more energy efficient. When an insect seeks a *target* (resource) this will be enveloped in a larger '*active space*' in which it can be perceived (Wilson, 1970). So two sequential search objects exist: (i) an *envelope of effective perception*; and (ii) the *target itself*. Flight behaviour is different in each case. For visual detection we assume the probability of detecting an active space is unaffected by the insect's air speed. Since the target is visible from about the same distance in all directions, this space will be broadly sub-spherical. But perceptive powers vary. HISC insects (Section **10.2.4.1**) have greater visual acuity and so much larger active spaces than LISC ones. The size of an active space also depends on the size and reflectance of the target, which varies with light intensity and contrast.

Concerning olfaction, which is unconstrained by light, the active space will be often an elongated, irregular plume, drifting in the air and irregular because of turbulence near the ground (Kennedy, 1983; Dusenbery, 1989; Cardé and Minks, 1995; Cardé, 1996). In stronger winds the plume is straighter and more concentrated (Cardé and Willis, 2008). Consider moths searching at night. The direction they move is unknown but the flight path should be fairly straight. Models (Dusenbery, 1989) suggest that they should fly straight at some vector of downwind (increasing speed and reducing fuel cost) to crosswind (increasing encounter rate at a given speed). This would be ~50% more effective than random flight. But there is much variation. Crosswind flight occurs in three parasitoid wasp species leaving a brassica crop (Williams *et al*., 2007), but the wasp *Venturia canescens*, searching for hosts, does not fly like this (Desouhant *et al*., 2003). Then, winds that change direction alter the search pattern: sometimes downwind searching is preferable (Reynolds *et al*., 2007; Guichard *et al*., 2010). Of course, the insects studied must be in the appetitive, not the redistributive, behavioural phase.

When within the active space moths show anemotaxis, flying upwind when chemically stimulated. Then, because of the shape of the wind profile (above), they are expected to fly near the ground to maximize their speed. In some species males can locate nubile females from ~10 km (Dudley, 2000). Since wind variation and turbulence disturbs odour plumes, an *internally generated* side-to-side 'counter-turning' is needed to follow them to source (Kennedy, 1983; Cardé, 1996). This can comprise a narrow, upwind 'zigzagging' or a wide casting across wind. Turbulence affects flight navigation and leads to patchy distribution of the attractant. Specialized receptors on the antennae of male *Manduca* respond uniquely to these *intermittent signals* (Hildebrand, 1995).

Moths such as *Adoxophyes*, *Grapholitha* and *Spodoptera* employ casting behaviour. Diffusion within the odour plume is slow so that far downwind, patches of strong odour are conserved. The optomotor reaction (see above) may be used to determine wind direction (Cardé and Willis, 2008). But strong winds disrupt the plumes and make flight difficult (Sattler, 1991). Gentle, low-level air streams transport the chemical messages more effectively. *Pimpla* females arrive *en masse* at the broken cocoons of their host the brown tail moth, an event mediated via air movement. Predators of lucerne aphids find them by responding to wind-borne indole acetaldehyde from their honeydew (van Emden and Service, 2004).

Heavy rain modifies wind patterns (Barry and Chorley, 1995), but also causes flooding. This is *locally* severe in high-gradient streams but *regionally* severe in extensive areas drained by large rivers. Flooding is a function of the amount of rain in the catchment and the nature of the topography. Much of the aquatic fauna is washed downstream, and mosquito larvae in marginal pools and sessile *Simulium* larvae may be affected (Section **7.3.2.4(h)**). When insects are thus displaced by wind or water, they lack control and risk being killed (Section **10.2.3.6**), another complex interaction, one between mechanical factors, topography, movement and survival.

Finally, we note that leaf-cutter ants respond to magnetic fields (Banks and Srygley, 2003), namely a further physical factor. Some birds, such as the robin, *Erithacus*, also have this capacity. It also occurs in honey bees (Frier *et al*., 1995, in Collett, 1996) and needs further investigation, particularly in the aculeate Hymenoptera.

10.2.4.6 Movement: Biotic factors: Population density

High population density often induces dispersal (Nicholson, 1933; Strong and Stiling, 1983; Enfjall and Leimar, 2005). It may also induce the development of polymorphic, dispersive forms, although these can be the direct result of genetics (Sections **10.2.4.1** and **11.2.3.1**). Again, these results are a primary effect of density, but affect only some species (Section **10.1**). In exopterygotes, crowded nymphs of locusts (*Schistocerca*, *Locusta*) develop into the migratory phases (Ellis *et al*., 1965; Uvarov, 1977; Section **5.2.1.1**). Similarly, crowding in some aphids (Bonnemaison, 1951; Toba *et al*., 1967), in a plant hopper (Kisimoto, 1956) and in *Adelges* spp. (Eichhorn, 1969) induces the development of a migratory morph. In endopterygotes, the eulophid wasp *Melittobia* (Section **8.2.2.5(p)**; Schmieder, 1933; Freeman and Ittyeipe, 1982; Silva-Torres and Matthews, 2003) develops flightless 'crawlers' at low density. These search adjacent cells of their aculeate victims. In *M. australica,* those at intermediate densities, the short-winged 'jumpers', search for other hosts nearby. The long-winged 'fliers', which develop ultimately at high density, are compulsive migrants. So emigration is density dependent, the three morphs being adapted to three levels of space: centimetres, metres and kilometres (Freeman and Ittyeipe, 1993; Sections **9.3** and **12.2**). Other trimorphisms occur in the ichneumon *Sphecophaga* (Donovan, 1991, in Godfray, 1994), several Hemiptera (Reuter, 1875), in the cricket *Melanogryllus* (Sellier, 1954, in Harrison, 1980), in *Aphis fabae* (Taylor, 1975) and *Lymantria dispar* (Keena *et al*., 2008). Oddly, however, Jackson (1958) found in the sub-aquatic mymarid wasp *Caraphractus* that crowding induces brachyptery. But in the so-called trimorphic ichneumon *Gelis corruptor* all females are genetically apterous, quite unlike *Melittobia* females, while aptery in males is induced by inadequate food (Salt, 1952).

While in many insects high density is the ultimate factor inducing the winged form, the proximate cause may be physical contact between juveniles, as in *Melittobia*, or a reduction in food quality. The latter is often due to intensive feeding, but may result from seasonal effects on the food plant (Section **10.2.4.7**), at which time the focal species has developed dense populations. This occurs in locusts (Uvarov, 1977) and aphids (Bonnemaison, 1951; Lees, 1966). Rarely, emigration may be inversely density dependent, as in *Melitaea cinxia* (Kuussaari *et al*., 1996). Density-dependent emigration in population processes is considered further in Section **12.3.4.3**.

10.2.4.7 Movement: Biotic factors: Food

Food finding is the greater part of resource finding. It is diverse in detail in relation to the many ways in which herbivores, carnivores, micropredators (Section **7.1.1.1**), parasitoids and detritivores obtain their food. Even so, visual and chemosensory cues, often in that order (Yamamoto *et al*., 1969), form key links in the chain of behaviour (Section **10.2.4.5**). Some insects seek non-trophic reproductive resources, such as dead wood, leaf pieces, resin and mud. Male euglossine bees collect fragrant compounds from orchids (Ackerman, 1983; Section **8.2.1.1**). And of course individuals seek, or are sought by, potential mates. Feeding and reproduction, however, may entail a conflict of interest. Indeed, in some groups adults do not feed during breeding, examples being gypsy moths (Section **5.2.1.4(f)**), nematoceran flies such as *Tipula* (Section **3.2.1.2(f)**) and the cyclorrhaphan bots (Section **7.4.1.1**).

These sequences interest us since pests searching for food plants, enemies (Coccinellidae, Parasitica, Tachinidae) searching for victims, and micropredators waylaying vertebrates for blood, follow such repertoires. While affected by the light and chemical environments in which they operate (Endler, 1992), insects generally move through decreasing spatial levels to reach their food. Flight is used at greater levels, and often walking at lesser ones, until the target is found (Section **10.2.4.5**), when they stop. Thus, honeydew acts as an *arrestant* for coccinellid larvae searching for aphid prey (Carter and Dixon, 1984; Section **8.2.2.4**(e)). In terms of sensory anatomy, note that the olfactory system, used before landing on a resource, is separate from the gustatory system, used for tasting it (Chapman, 1999). So it is often effective to disrupt these mechanistic sequences in pests as a means of economic control. As winged, adult insects have far greater capacity to scan the environment for resources than do their juveniles, we consider three distinct areas: (i) the appetitive search for suitable food for the individual itself during the favourable season; (ii) the effects that quantity and quality of food may have on subsequent dispersal or migration, generally of the adults, and often at the end of the favourable season; and (iii) for adult females, the search for food for the progeny, which is better dealt with under reproduction (Section **10.2.5.2**). The first may involve aggregative behaviour, causing increasing density; (ii) and (iii) often result in reduced density, relative to that at the source (Taylor and Taylor, 1977).

In most orthopteroids and hemipteroids nymphal and adult foods, and so the search processes for them, may well be similar (Bryant, 1969). This principle is true for a few endopterygotes, especially chrysomelid beetles. But in the aquatic palaeopteroids and in most endopterygotes, juvenile and adult foods are different (Wäckers *et al*., 2007) and so require separate search patterns. Of course, in the latter group the pupa permits extensive restructuring of the body (Section **1.5**). Then, according to phenology, these searches occur concurrently or alternately.

But some adults require a variety of foods, as do gypsy moth larvae (Section **10.2.2.5**). For ovipositing parasitoids nectar is critical (Section **13.2.4.7**), although female Parasitica often feed on their victims, typically individuals they do not parasitize (Howard, 1910; Thompson and Parker, 1928a; de Bach, 1943; Kidd and Jervis, 1996). Insects needing nectar are frequently limited by low temperature and more specifically by lack of insolation (Willmer, 1983), so there is a sequential interaction between a physical factor and a biotic one, as we have seen is often the case. Earwigs (Section **6.2.1.1(a)**), which consume insect pupae, juvenile moths on trees, pollen and petals, while rather primitive in gross structure, must possess a sophisticated diversity of search and selection behaviours.

After maternal distribution of the eggs (Section **10.2.5.2**), nymphs and most larvae seek their food only at the patch level (Southwood, 1977; Sections **9.3** and **12.2**). But initial congregation may change to dispersal within a limited ambit. Thus the nymphs of *Nezara* and the larvae of several sawflies and lepidopterans (Sections **6.3.2.1(a)** and **10.2.3.7**), are gregarious when young but solitary when older, and hence spread themselves out on the food resources or seek new ones, so reducing their own density. Additionally, induced plant defences (Section **2.4.2**) may dictate a dispersed pattern of herbivory.

Finally, low food quality may induce redistribution, although such an effect is often consequent on high density on the food patch, with which it may be confounded (Section **10.2.4.6**). In aphids, poor food quality often induces the production of dispersive alates (Johnson, 1966). Crowding of juveniles on the food leads to emigration in locusts (Section **5.2.1.1**), some aphids (Section **3.3.2(a)**), delphacid bugs (Strong and Stiling, 1983; Iwanga and Tojo, 1986), *Melittobia* (Section **10.2.4.8**) and a fritillary butterfly (Enfjall and Leimar, 2005). While high density is often the major cause of dispersal, if food were superabundant crowding might not ensue. Young winter moth larvae, noted above, disperse more actively when they cannot find food (Wint, 1983), although this is often due to a mismatch in the times of eclosion and bud burst (Section **10.2.5.2**).

10.2.4.8 Movement: Biotic factors: Enemies

Apart from defensive morphology and parental care (Gross, 1993), defence against enemies depends on the perception of danger and escape movement. Such movements often have an unpredictable component (Section **9.4.3.7**). They can be escape reactions (*evasions*) or vigorous efforts of potential victims to deter enemies, culminating in what can be called *aggressive defence*. Due to centrifugal dispersal of threatened individuals there may be density effects. As in many mammals, recognition of enemies by potential victims often depends on olfaction. This is mediated by kairomones transported by the wind (Section **10.2.4.5**) and detected by sensilla on the antennae. Insect eyes, however, detect moving objects well, the latter generally inducing escape reactions in mobile instars. For evasion, in several groups individuals jump when disturbed, using modified hind legs. Probably because of basic differences in development (Section **1.3**), both nymphs and adults jump in exopterygotes (grasshoppers, cicadellid bugs). But in endopterygotes (fleas, flea beetles and flea weevils), only adults jump. Jumping for escape is also found in some small moths in the Gelechioidea and Tortricoidea, some species of which can also fly while others cannot (Sattler, 1991). Other juveniles simply drop when disturbed and adults that cannot take flight quickly, like phytophagous beetles, often do so too. Dropping may be combined with feigning death, a deception inversely related to temperature in *Callosobruchus* (Miyataki, 2008). Finally, the wing scales of Lepidoptera assist in their freeing themselves from spider's webs (Wootton, 1992).

But there are more specialized means of defence and escape (Witz, 1990). Cutworms, *Hyperia* and *Tipula* larvae when attacked, for example by carabid beetles, bend their bodies into a C-shape and rotate about their own axis. Some caterpillars thrash when attacked (Gross, 1993). Applying the rationale that attack is the best defence, workers of social Hymenoptera, bombardier beetles and some other species combat aggressors. Aphids kick their parasitoids, thus deterring oviposition (Gross, 1993). The solitary wasp *Pachodynerus nasidens* will crush the parasitoid of its larvae, *Melittobia*, in its mandibles. Locusts secrete noxious oral fluids (M.A. Freeman, personal communication); thrips do so from the anus. Bombardier beetles eject an evil-smelling fluid from perianal glands, as do some chrysomelid and coccinellid beetles from their leg joints and some notodontid caterpillars from a ventral prothoracic gland. Larvae of *Caligo memnon* (Nymphalidae) spray attacking ants with a noxious fluid, synthesized in prothoracic glands (Eisner, 1970, in Dyer, 1995). The grasshopper *Poekiloceros bufonius* squirts offensive compounds, derived from its milkweed food, at aggressors (Rosenthal, 1986). *Heliothis* larvae use similar tactics against their parasitoids. The bug *Anasa tristis* employs a lethal spray against tachinid flies (Dietrick *et al*., 1957, in Gross, 1993). Larval *Anthrenus flavipes* (Dermestidae) deter the bethylid parasitoid *Laelius pedatus* with their anal setae (Ma *et al*., 1978). The ant *Crematogaster brevispinosa* under attack emits an evil odour from the abdomen, which other conspecific ants copy.

Apart from such immediate responses (Section **10.2.4.1**), Sloggett and Weisser (2002) describe an interesting delayed response between the aphid *Acyrthosiphon pisum* and its parasitoid *Aphidius ervi*. While parasitized nymphs fail to develop wings, the presence of female parasitoids among the others causes increased production of dispersive alates. Predatory ladybirds also induce this effect. *Myzus persicae* emits an alarm pheromone when attacked, causing the colony to scatter. *Frankliniella* seek refuges when they receive odours from conspecific thrips under attack by the bug *Orius* (Dicke and Grostal, 2001).

10.2.5 Reproduction, particularly fertility and fecundity

10.2.5.1 General introduction

Reproduction is the most complex attribute to examine. Apart from effects on adults arising from their growth and survival when juvenile, it comprises a sequence of events in adult physiology and behaviour: time to maturity, gonadal maturation, flight, mate finding, mate selection, fertilization, and egg production and distribution. These are all affected by physical factors and often by biotic ones too. For the latter, food has a critical role and we will deal with this in Section **10.2.5.2**, after looking at some generalities. As G.C. Williams (1987) put it in a related context: ‘There really are many possible kinds of understanding of a topic …’.

For maturation, recall that while many non-feeding adults mate shortly after emergence, a majority has a pre-reproductive period in which flight and reproductive capacity develop, well shown in some dragonflies (Marden *et al*., 1998). Of course, mate finding, selection and fertilization define the limits of a species (Paterson, 1982; Walter, 2003). While *isolating mechanisms* are crucial in speciation (Section **9.10**; Mayr, 1963), what is relevant today for mature adults is to find a *suitable mate(s)* speedily. But conflict may exist between the imperatives of sexual selection and those of natural selection (Andersson, 1994; Section **9.1**). A showy male manifesting his good genes (Hamilton and Zuk, 1982) may also attract enemies (Endler, 1992; Kunte, 2008). This risk has been examined for butterflies (Oliver *et al*., 2009), but it has long been known in light-signalling fireflies and the calling cicada *Okanagana* (Section **3.3.2.1(a)**). Chirping crickets to their detriment attract tachinid parasitoids. Since evolution continues (Haldane, 1954; Trivers, 1985), one expects it to maximize the *rate* of mate finding under *existing* conditions. This means developing safe intraspecific signalling (e.g. highly specific pheromones; Zuk and Kolluru, 1998), so reducing mortal risk just before reproduction and improving the ways to assess mate suitability, of which there are several aspects.

When females are able and/or live long enough to choose their mate, they may prefer like, or unlike, males. In the former, assortative mating tends to produce like offspring, reduced heterozygosity and variation. In the latter, disassortative mating leads to greater heterozygosity and more variation (Section **9.6**). Choice can be frequency dependent, rare males being preferred, as in some *Drosophila* (Ehrman, 1966, 1970), sometimes in our own species, and a type of disassortative mating. Size-related assortative mating occurs in *Neacoryphus* (Lygaeidae) (McLain and Shure, 1987), *Epirrita autumnata* (Geometridae) (Haukioja and Neuvonen, 1985), *Parasemia plantaginis* (Arctiidae) (Gordon *et al*., 2015) and some desert tenebrionid beetles. There is even selection for large males in some dipteran mating swarms, as they fly at the top where nubile females usually enter. In some midges small males mate below the swarm (McLachlan and Neems, 1989). When contest exists between males for mates, small males are sneaky and often have the advantage of maturing early. Such strategies, like those in foraging, vary greatly in a species (Wilson, 1998).

For *egg production* we include the efforts of both sexes since the *genetic contribution* of the sexes to each offspring is normally about equal. Males often contribute materially to AF in other ways (Shorey, 1963; Scott, 1998; Gillott, 2003). *Fecundity* is the number of offspring, normally eggs, a *female* deposits in her lifetime. The number of *viable* ones produced is her *fertility* (Awmack and Leather, 2002), an accurate measure of reproductive output. In sparse populations some females remain unmated, an Allee effect, and inbreeding depression and genetic drift (Stevens *et al*., 1999; Walter *et al*., 2015; Section **11.2.3.1**) may ensue. Of course, genotype influences fertility (Watt, 1992), and genetic conflict within the genome (Burt and Trivers, 2006) can reduce it.

In nature, *only a proportion* of emerged females breeds at all. So their survivorship, especially during redistribution (Section **10.2.4.1**), has a major influence on the mean fecundity achieved by the population (Freeman, 1973a, 1976, 1977, 1981a; Freeman and Ittyeipe, 1993; Leather, 1988). Non-migrant species (Section **12.3.4.4(c)**), especially pro-ovigenic moths like bagworms, gypsies and *Epirrita* (Tammaru *et al*., 1996) (batch layers), and crane flies and gall midges that oviposit soon after emergence and mating, are likely to lay a high proportion of the eggs (Courtney, 1984). In the midge *Rhopalomyia californica* >80% of non-migrants laid most of their eggs (Rosenheim *et al*., 2008). But bad weather can prevent mating, kill *immature adult females* directly or extend their immaturity, when many die from other causes. As above, bad weather *during the oviposition period* can kill them, prevent or delay egg laying (Section **10.2.4.7**) as in Hessian flies (Section **4.4.1.1(f)**) and *Anthocharis*.

For dynamics, the percentage of female *Choristoneura* that lay was estimated by comparing observed and expected egg numbers in the field (Morris, 1963), and due to dispersive loss, predation and failure to mate, was found to be only about 50%. But a better, time-independent method exists if fertility and juvenile mortality can be sampled widely in space and time (Freeman, 1976, 1982). Suitable cases are cell-building solitary wasps, gall midges and bark beetles. The estimate for *Sceliphron* in Jamaica at 116 locations and >30 generations is that about one in three emerged females lays eggs (Freeman, 1977). For a similar wasp, *Trypoxylon palliditarse* in Trinidad, it is about one in six (Freeman, 1981a). Danks (1971b) for some British solitary wasps, Smith (1979) for *Sceliphron laetum* in Australia and Watmough (1983) for carpenter bees in South Africa, suggest similar results. For small, frail insects, like gall midges (Freeman and Geoghagen, 1989; Briggs and Latto, 2000), some parasitoids and aphids, the proportion breeding is far less. For the flying morph of *Melittobia*, the figure is <1% (Freeman and Ittyeipe, 1993). Then, by comparing autumn and spring densities of *Rhopalosiphum* (Section **5.3.1.2**(**h**)), Ward *et al*. (1998) estimated the ratio of successful autumn migrants at 1 in 168.

When assessing population growth (Section **11.5.2.1**), the time of first egg laying (Cole, 1954) and the *rate* at which they are laid are of major interest. MPF is normally a function of female size and the number of her ovarioles (Price, P.W., 1997; see below), the latter being, at least partly, under genetic control. But natural selection does not tend simply to maximize the birth rate: it maximizes the *difference* between birth and death rates (Birch, 1960). Of course, higher birth rate may permit greater difference (below). A further long-standing argument arising from host/parasitoid models is whether AF is limited by egg supply or, recalling that suitable oviposition sites must be found, by time available to lay them. Thompson (1924) assumed egg supply to be paramount in parasitoids. Nicholson and Bailey (1935), following Lotka (1925), assumed time limitation (Section **11.5.2.3**). But both may be involved (Rosenheim, 1999b). Then in a field study, egg-laying rate by a mymarid wasp was far less than the maximum, since females did not oviposit in ostensibly suitable host bugs, leaving to investigate other patches (Cronin and Strong, 1993). Here, egg distribution constrained AF and may well do so in many other cases.

The pattern of egg production differs greatly in different groups. As in Johnson's oogenesis-flight syndrome (Section **10.2.4.1**), this has basic outcomes for reproductive behaviour and dynamics. When species emerge with a full complement of mature eggs (*pro-ovigenic*), as in crane flies, gall midges and non-feeding moths, migration is minimized. If pre- and post-reproductive females can be collected the dissection of representative samples estimates both MPF and AF. Sometimes all the eggs are deposited in one batch (Myers, 1988; Section **10.2.4.6**). Such females are purely *capital breeders* (Stearns, 1992), using only nutrients acquired during the larval stage. But *synovigenic* insects take time to mature eggs. While most Lepidoptera emerge with a full load of eggs (Wheeler, 1996), these are variously developed (Oberhauser, 1997; Awmack and Leather, 2002). Indeed, synovigeny can be variable (Jervis *et al*., 2001). MPF can still be estimated by dissection. In many beetles, egg development is initiated by adult feeding, as in *Apion* (Section **6.2.1.2**(**b**)), and AF determined mainly by the amount eaten (Section **10.2.5.2**). Such insects are *income breeders* (Stearns, 1992). Syrphine flies (Schneider, 1969) and *Apion* weevils (Freeman, 1967a) do not develop ovaries until they have eaten pollen. In the ladybirds *Coccinella* and *Menochilus*, daily fecundity is related to the amount of aphid food consumed (Dixon and Agarwala, 2002). In *Menochilus* the egg biomass laid may reach six times that of the female's initial body mass. In *Danaus plexippus* (Danaidae), while larval reserves are used for maintenance, income during adult life largely determines AF (Oberhauser, 1997). Spermatophores donated by males have little effect (Svärd and Wiklund, 1988). In fact, many insects use a mixed strategy of capital and income, for example in *Eupelmus* (Section **8.2.2.5**(**q**)) lipids are *capital* while sugars are *income* (Casas *et al*., 2005).

Female size within species (Section **10.2.5.2**) should be measured, being usually related to the number of ovarioles and thus to MPF (Hodĕk, 1993), as it is in the parasitoid wasp *Encarsia formosa* (Hoddle *et al*., 1998) and the Caribbean grasshopper *Orphulella punctata* (Freeman, unpublished data). In species that mature several egg batches, such as grasshoppers and mosquitoes, dissection can still be used, but it is hard to get good estimates of the number and size of batches laid. Traces in the ovary, however, may allow the number of ovarian cycles completed to be measured, as in mosquitoes and tsetse. While AF in caged females can be used, some species perform poorly. Conversely, estimates of AF of 'culture-friendly' populations in the laboratory, where natural hazards are reduced and migratory losses cannot occur, are often much greater than those in the field.

Field AF varies widely between insect groups. There is often an inverse relationship between fecundity and egg size. It varies from a single, relatively large egg in the oviparae of eriosomine aphids and the grape phylloxera (Sections **3.3.3.1**(**a**) and **5.3.1.2**(**g**)) and <10 in many solitary wasps and bees, to >3000 in some scale insects and >10,000 in the moth *Abantiades* (Section **3.2.1.2**(**d**)) and those tachinid flies and eucharitid wasps that scatter microtype eggs (Section **8.2.2.5**). A typical value is 100–150. In some outbreaking forest moths, eggs laid early have more yolk than those laid late (Szujecki, 1987). In several other cases early eggs are *larger* and have more yolk than late ones (Mousseau and Dingle, 1991), which enhances the size and survival of the early offspring. A trade-off exists between the number of eggs laid and the investment given to each one (Darwin, 1871; Smith and Fretwell, 1974). Investment is often expressed in relative egg size, varying both within and between species (Fox and Czesak, 2000), as in carabid beetles (Juliano, 1985; Wallin *et al.*, 1992) and solitary bees (Kim, 1997). In solitary aculeates and dung beetles the investment/egg given as provisions is high, but AF is low. High parental investment requires complex behaviour. Conversely, when the risk to an individual egg is intrinsically high, large numbers are produced, the *principle of balanced mortality* (Cole, 1954; Godfray, 1994; Price, P.W., 1997). Some species lay fewer, larger eggs if the offspring will face harsh conditions, as in the grasshopper *Chorthippus brunneus* (Cherrill, 2002). For Australian dacine flies, polyphagous species usually have more ovarioles and so are more fecund than specialist species (Fitt, 1990). In all, there is great variation.

Generally, then, the greater the AF the less chance each offspring has of reaching maturity. But this principle does not always hold as the *fecundity/mortality* ratio is very variable (Section **12.4**). In North Carolina, the AF of *Conotrachelus nenuphar* (Section **6.2.1.2(d)**) is ~140, but juvenile mortality only ~67% (Mampe and Neunzig, 1967). In Corfu, that of *Dacus oleae* (Section **6.3.1.1(p)**) is ~300, but larval mortality often <30% (Kapatos and Fletcher, 1986, in Fletcher, 1987). In *Eupelmus* (Section **6.3.1.2(b)**) AF is >200, but mortality only ~39% (Doury and Rojas-Rousse, 1994). *Melittobia* (Section **8.2.2.5(p)**) is similar, but even more extreme. *Conophthorus resinosae* (Section **6.3.1.1(c)**) suffers little mortality from enemies, but high temperatures and food shortage kill juveniles periodically (Mattson, 1980a). Naturally, the above situations result in rapid population growth unless otherwise constrained, especially by losses incurred in redistribution and resource location.

It has been suggested across animal species that r_m, the intrinsic rate of increase, in which fertility plays a big part, is related inversely to body size (Smith, 1954). This can be true for insect subclasses, but within related groups such as families there is little evidence for it (Gaston, 1988). Endophytic insects tend to be smaller than exophytic ones and have lower AF (Cornell and Hawkins, 1995), but this applies only to those constrained in soft stems and leaves. Goat moths (Section **4.2.1.2(m)**), some other wood-boring moths like *Paysandisia archon* and *Aenetus virescens*, many cerambycid beetles (e.g. *Titanus giganteus*; Hamilton, 1996) and siricid sawflies, are large or very large. This fact gives substance to our separation of such feeding environments in Chapter 4.

10.2.5.2 Reproduction: Biotic factors: Food

The amount of quality food a female consumes during development, and in synovigenic species prior to and during egg laying, are key in determining fecundity (Dempster and Pollard, 1981; Juliano, 1986; Hoděk, 1993; Wheeler, 1996; Smith and Lamb, 2004; Wäckers *et al.*, 2007). Food intake also has outcomes for male reproductive performance. In both sexes size and its attendant qualities largely determine RS, as in *Mayetiola* (Section **4.4.4**; Harris *et al.*, 2001). Finally, the egg distribution achieved by females often affects the fate of the progeny, the PPL (Section **10.2.3.8**). So here we break with normal procedure and examine effects of the biotic factor *food* on an innate attribute before those of physical factors, although these have major influences on reproductive physiology and the behaviour associated with it. Indeed, they considerably complicate the overall picture of reproduction. But generally, both males and females within a species that are better fed are normally larger, survive better and have greater RS, in the sequence:

$$\text{Food} \rightarrow \text{Growth} \rightarrow \text{Size} \rightarrow \text{Survival} \rightarrow \text{RS}$$

Thus, growth and female size in species are usually positively correlated with the number and rate of egg laying (Spradbery, 1977; Freeman and Johnston, 1978a; Juliano, 1985; Banno, 1990; Kim, 1997; Alto *et al.*, 2008; Berger *et al.*, 2008). In *Aedes aegypti* small, under-fed females find prey (food) poorly (Bowen, 1991) and may lay fewer eggs. In the aphid *Pemphigus betae*, large fundatrices have more and larger progeny than small ones do (Whitham, 1980). We also expect genetic factors to be involved (Watt, 1992; Leather and Awmack, 1998). Despite this general trend, fecundity is unrelated to body size in *Gerris buenoi* (Gerridae) (Klingenberg and Spence, 1997). The authors point out, however, that size evolves as 'a correlated response to selection on other traits'. This may be an attribute of a peculiar population, however, as other workers did not get this result

(Sokolovska *et al.*, 2000). In general, large males tend to have higher RS too, but this is less well studied.

Even so, the direct link between food and AF is clear in *Calliphora* and *Lucilia*. When their maggots feed on a big carcass, emerging females are large and fecund. But when food is insufficient they have evolved larvae that can pupate at much less than full size. Any factor reducing the quantity and/or quality of their food, such as that found in an old carcass, or competition, would have this effect. Similarly, the aphid-eating larvae of *Taraka hamada* (Lycaenidae) can pupate when small (Banno, 1990). While AF of small females is low, the eggs they lay still carry parental genes to posterity. So, early metamorphosis and reduced fecundity have been selected for in preference to death and zero fecundity. In *Sarcophaga* spp. flies that breed in dead snails, the size of their puparia decreases with number per snail. But when only a single species is present, the puparia are all of similar size, suggesting that they apportion their limited food instead of competing for it (Beaver, 1973). Siblings doing this maximize parental fitness. Food plant quality also has effects, as in forest moths (Section **10.2.2.5**). In *Calvia quatuor-decimguttata* (Coccinellidae) AF varies greatly according to prey species, being 143–198 on *Psylla mali* but 28–46 on *Hyalopterus pruni* (Semyanov, 1980, in Nedvěd and Honěk, 2012). Large females in a population are often *twice* the mass of small ones, and *more than twice* as fecund (Shorey 1963; Freeman and Johnston 1978a; Freeman and Geoghagen, 1987; Gilbert, 1984; Sopow and Quiring, 1998).

Continuing with blow flies, since maggots that hatch late are more likely to suffer the effects of shortage, a fast food-finding strategy has evolved in the adult females (Dethier, 1961; Section **10.2.4.1**). Eggs hatch quickly (some species larviposit), and the larvae feed rapaciously. As the Confederate general Nathan Forrest said of military strategy: 'Git thar the fastest with the mostest'. Arriving quickly also means that females can locate food rapidly between laying egg batches, which with their habit of basking (Section **10.2.5.1**) enhances fecundity. Fast arrival also effects competition (Section **10.2.1**). In Finland, *Lucilia illustris* emerges first in the year, most likely an advantage over other blow flies (Hanski, 1987). The big muscid fly *Mesembrina meridiana* lays single, relatively huge (~4.5 mm) eggs that hatch immediately in dung (Séguy, 1923). They are much bigger than those of *Calliphora vomitoria* (~1.5 mm), a fly of similar size. The large larva that hatches may be better able to defend itself in so dangerous a medium, perhaps an example of 'the mostest'. Even lumbering burying beetles *Nicrophorus*, find carcasses quickly (Wilson *et al.*, 1984; Scott, 1998; Section **12.3.4.3**). A similar relationship occurs in competition between hyperparasitoids (Zhu *et al.*, 2016) and in larval competition the dung beetle *Aphodius ater* (Hirschberger, 1999). Again, in biocontrol and in trap cropping (Section **13.2.4.4**), having the pest's enemies *present early and in numbers* favours successful control. We label this principle '*Forrest's maxim*'. More generally, a focal species should be at the right place at the right time to maximize its RS (Section **2.1**; see Section **11.4.4.2**).

A temporal aspect of egg distribution must be recognized. Of course, capital breeders (Section **10.2.5.1**) lay eggs just after emergence, while income breeders lay them over a longer period, allowing more time for effective distribution. Then eggs are generally laid either during the day or at night. Oviposition in *Aedes aegypti* is crepuscular, the majority being laid in the evening, the minority at dawn (Chadee, 2010). Laboratory trials show that if a female fails to find a suitable site for a few days, it then dumps the eggs at the first place it finds, rather than spreading them between several places. Its risk-spreading behaviour (Section **9.7**) is compromised.

Leather (1988) cautioned that there are pitfalls in relating female 'size' to her fecundity. Thus, pupal mass in moths is often used as a predictor, but because of weight loss during development, length and/or width are preferable measurements. None the less, there is a close correlation between pupal mass and fecundity in larch budmoths (Baltensweiler *et al.*, 1977; Section **5.2.1.4(d)**) and in *Epirrita autumnata* (Tammaru *et al.*, 1996). But a full complement of eggs is seldom laid (Leather 1988; Section **10.2.5.1**), AF is <<MPF. *Panolis flammea* (Section **5.2.1.4(g)**) in Scotland lays only 28%. In addition, female size may influence fertility, as in codling moths.

Food for adults affects AF in three ways (Wheeler, 1996; Boggs, 1997). First, females may not feed at all, which is common in pro-ovigenic species. Examples occur in the Diptera (Cecidomyiidae, Tipulidae, *Gasterophilus*, *Oestrus*) and in moths with atrophied mouthparts (Psychidae, Lasiocampidae). Here females emerge with a complement of mature eggs ready to lay, they need only be mated. They are short lived and, genetic factors aside, *their potential fecundity is determined largely by their developmental history*. Second, females lay some eggs if they do not feed but more if they do. Autogenous culicid, simuliid and ceratopogonid flies (Section **7.3.2.4**), larch budmoths (Baltensweiler *et al*., 1977) and some butterflies (Boggs, 1997) are examples. *Potential fecundity is determined by their developmental history and by conditions during adulthood*, *especially food supply*. Some females, such as *Aedes communis* (Hocking, 1952) and *Apion dichroum* (Freeman, 1967a), autolyse their flight muscles prior to oviposition, probably using the material to boost oogenesis. This transfer has been documented in *Dysdercus cingulatus* (Pyrrhocoridae) (Nair and Prabhu, 1985, in Marden, 2000). Several moths and flies have alate males and apterous females, the latter presumably diverting nutriment into oogenesis (Roff, 1990). Third, in some locusts, coccinellid beetles, weevils, solitary wasps, many parasitic wasps and muscid flies, adult females cannot lay eggs unless they feed. Most blow flies do not mate or lay eggs until they have taken a protein meal (Norris, 1965). Even so, an autogenous strain of *Lucilia cuprina* (Section **7.4.2.1**) exists (Kerswell and Burd, 2012). Barring accidents, their life spans are relatively long. When they feed, especially on protein-rich foods, MPF *is again determined partly by developmental history and partly by food as adults* (Boggs, 1997).

In all cases genetic factors may be involved (Conner, 2003; Burt and Trivers, 2006), although this seems to be unimportant in *Sceliphron* (see below; Freeman, 1981c), *Tyria* (Dempster, 1982) and *Epirrita* (Tammaru *et al*., 1996). Feeding on nectar, which often contains amino acids (Section **8.2.1.1**), increases AF in many butterflies (Wheeler, 1996). In *Heliconius*, adults deprived of pollen die young and AF is lower (Gilbert and Singer, 1975, Boggs, 1997). *Heliconius* steep pollen in nectar and imbibe the amino acids that diffuse out (Gilbert, 1972, in Baker and Baker, 1973). Nectar feeding extends life and AF of *Anopheles gambiae.* But when *Calathus melanocephalus* (Carabidae) eats the toxic larvae of the heather beetle *Lochmaea suturalis* when these are abundant, AF is reduced (den Boer, 1998). In this family, quantity and quality of food greatly affects AF (Wallin *et al*., 1992), but may take months to be apparent (Juliano, 1986). In *Brachinus*, well-fed females lay about tenfold more eggs than under-fed ones. Also, predators (and some herbivores; see below and Section **10.2.2.5**) eating a *varied diet* are more fecund, another factor to note in models (Section **11.5.2.3**). But in *Encarsia* and *Melittobia* wasps AF relates to *host size*. In moths, individual egg weights may reduce as females age, as in *Tyria*, but this can be a statistical artefact due to eggs being smaller in the last batch (Moore and Singer, 1987). But in *Dysdercus fasciatus,* egg size increases and clutch size decreases as females age (Kasule, 1991).

In *Sceliphron,* small females (70 mg) lay ~5 eggs in the field, but large females (130 mg) often lay 15 or more, at a rate reducing with age (Fig. 10.22). Adult size is determined by the amount of food provisioned (Freeman, 1981b and c). But females must eat spiders to breed. Maternal size also influences the sex ratio in the offspring, large females producing a higher proportion of daughters. Thus, population growth, due to AF and sex ratio, is affected by the size distribution of breeding females. In the solitary bee *Megachile apicalis*, large females are more fecund and built and provisioned cells more rapidly, but unlike *Sceliphron*, lived no longer than small females (Kim, 1997). In the damselfly *Coenagrion puella*, survival is unrelated to reproductive output (Hassall *et al*., 2015). These authors mention body size briefly, medium, sized damselflies having the highest success.

The larvae of many moths are polyphagous and food quality, as judged by mean size and fat content of the pupae that result, varies a lot. In winter moths, mean pupal mass is different after feeding on any one of its several food plants: oak, hawthorn, apple, hazel and blackthorn (Wint, 1983) and has marked effects on MPF. Oak is the primary food plant and many of the others incidentals. In *Melanoplus bilituratus* (Section **5.2.1.1**(**d**)), AF plummets from ~170 on C3 plants to ~22 on C4 ones. But the time of feeding is also critical: larvae feeding later in the year often have poorer food. Various combinations of plant foods have a big effect on AF in gypsy moths (Section **10.2.2.5**) and also influence the amount of yolk donated to each egg. Further complexity exists in *Aonidiella aurantii* (Section **6.3.2.2**(**a**)). Food may affect sex ratio and in turn reproductive potential. When *Comperiella bifasciata* (Encyrtidae) attacks these scales, the type of food plant involved also influences its sex ratio (Smith, 1957). On yucca, sago palm and agave, three to five females per male were produced, but on citrus the ratio was near 1:1. Different food plants also confer various levels of resistance to parasitoids (Section **10.2.3.8**).

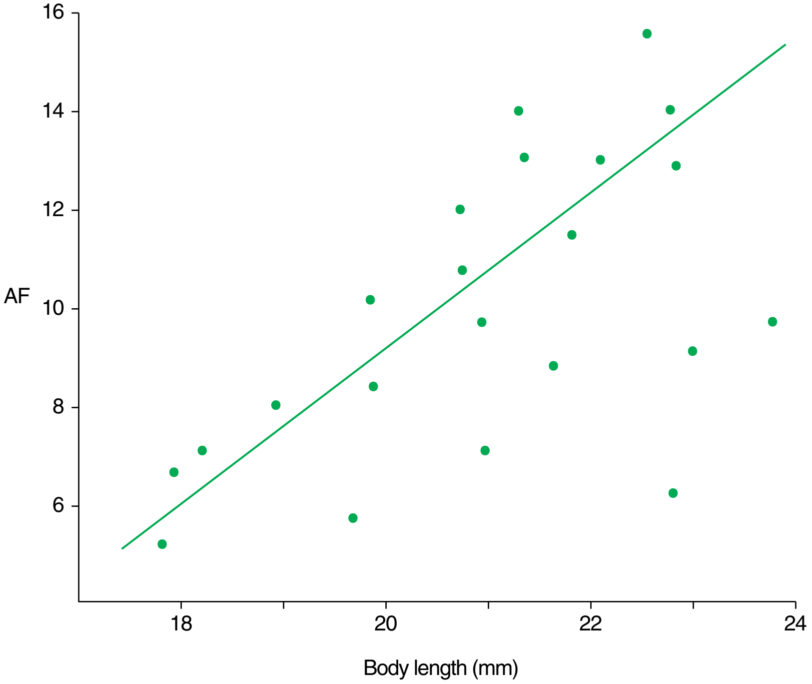


Fig. 10.22. Achieved field fecundity in *Sceliphron assimile*. Within a species of many solitary wasps and bees, size is largely a result of the amount of food provisioned by their mother. Subsequently, the fecundity the progeny achieve depends very much on size. Notice in the Fig., that while there is a fair linear fit to the data points, several of them lie to the bottom right of the line. These points relate to females who failed to achieve their potential fecundity, very probably because, although starting to lay, they were killed before reaching their potential. So the figure illustrates the interaction between fecundity and survival as well as between growth and fecundity. This should sensitize one to the possibility of further interactions between the attributes in any case under investigation.

Unravelling such complexity will improve our understanding the paradox of sub-optimal food plants being eaten (Ode, 2006). But the ability of insects to find a given food plant (Section **10.2.4.7**) in the limited time available to them must also be considered. Similar outcomes exist in polyphagous predators.

A major female function in most species is that of placing the progeny on or near an adequate food supply (Stamp, 1980; Section **10.2.5.3**), giving rise to the egg distribution. Searching by parasitoids was discussed in Section **8.2.2.1** and the PPL in Section **10.2.3.8**, but here the evolutionary expectation is again that 'mother knows best'. Namely she will choose the medium maximizing offspring fitness and thereby of herself and her mate(s). But other factors, both physical, biotic and involving a shortage of time (Levins and MacArthur, 1969; Rosenheim, 1999a and b) may intervene. Some parasitic wasps, herbivores such as butterflies (Dempster, 1992) and fruit flies produce an ODP (Section **10.1.2**), often deterring oviposition by later females on the same food item (but see van Alphen and Visser, 1990). The gall fly parasitoid, *Eurytoma curta*, avoids superparasitism efficiently (Varley, 1941). *Apion dichroum* (Freeman, 1967a) and the moth *Upiga virescens* (Holland and Fleming, 1999) oviposit non-randomly in food items, spacing the eggs singly. This may be due to an ODP. This behaviour often occurs when food resources are small and/or ephemeral (Dixon, 2000), as in Hessian flies. Even so, larval frass deters egg laying in the boring beetle *Monochamus* (Anbutsu and Togashi, 2002, in Harris *et al.*, 2006), where food is certainly not ephemeral. ODPs, especially in aggregate, waste the time of subsequent females and hence may reduce their AF, but they also prevent dangerously high densities for all parties. In time, however, rain may wash them off (Hoffmeister and Gienapp, 2001).

Similarly, organic volatiles emitted by plants may deter oviposition, as in *Manduca* attempting to oviposit on *Nicotiana* plants (Kessler and Baldwin, 2001) and in some fruit flies (Section **6.3.1.1**). Then, active feeding by larvae may deter egg laying by conspecific females, as in *Trichoplusia ni*, *Heliothis virescens* and *Manduca quinquemaculata* (from Hilker and Meiners, 2006). In some pierid butterflies whose larvae feed on cruciferous flowers, the eggs turn red rapidly. Since these insects can see red, although many insects do not, the obvious egg colour may deter oviposition by conspecific females, and so avoid competition for these limited resources (Shapiro, 1981). The egg clusters of some arctiid and zygaenid moths and lygaeid bugs are brightly coloured and toxic (Rothschild, in Stamp, 1980). In contrast, those of the bath white *P. daplidice* resemble the anthers of *Resida*, near which they are laid (South, 1906). Many other insects have cryptic eggs.

The type of egg distribution achieved depends on a female's ability to locate food for the juveniles. This ability varies greatly between different taxa, their ISC (Section **10.2.4.1**), with intraspecific differences, with prevailing weather (Sections **10.2.5.3** and **10.2.5.4**) and with food distribution, apparency and suitability (Wiklund, 1984; Section **2.4.1**). It is also an aspect of risk spreading or lack of it (Section **9.7**). First, female psychid, lasiocampid and lymantriid forest moths that do not feed and use stored fat for fuel, fly weakly or not at all and produce only one or a few egg masses (Hebert, 1983). They are short lived, putting their metabolic reserves into reproduction not into redistribution or appetitive behaviour. In addition, they are often little affected by the weather in their efforts and tend to have proportionately high AF (Courtney, 1984). Larvae emerging from such egg clusters usually form big sibling groups, which may have positive effects on their potential RS (Denno and Benrey, 1997) since they are often aposematic and distasteful (Sillén-Tullberg, 1988).

In other cases larvae effect further more extensive distribution. Several moths with flightless females that lay single egg masses have dispersive young larvae (Section **5.2.1.4(g)**). Then in large blues, *Maculinea* spp., females oviposit on specific plants, but final instar larvae fall to the ground and may be carried by *Myrmica* ants to their nests, where larvae complete development (Thomas, 1995; Anton *et al*., 2007). *Argynnis paphia* (Nymphalidae) lays eggs on the boles of trees, the larvae then seeking Viola food plants. Such behaviour is typical of butterflies overwintering as eggs whose larvae eat herbs that decay in winter (Wiklund, 1984). The triungulins of some tachinid flies (Section **8.2.2.5(h)**) and planidia of perilampid wasps are deposited near their hosts and complete the final search themselves. Similar patterns occur in young nymphs of cicadas and froghoppers (Sections **3.3.2.1(a)** and **3.3.2.1(b)**), young larval citrus weevils (Section **3.2.2.1(b)**), cane grubs (Section **3.2.1.2(b)**), cabbage root flies (Section **3.2.2.1(i)**) and wheat bulb flies (Section **3.2.2.1(j)**), allowing them access to food adult females cannot reach.

The egg-laying strategies of *Tipula paludosa* (Sections **3.2.1.2(f)** and **9.7**), and *Choristoneura* (Section **5.2.1.4(c)**) are peculiar: most eggs are laid at the natal site and a few elsewhere. Many moths lay a few to several egg batches (*Heliothis*, *Plutella*, *Tyria*,), and some butterflies, having ostensibly similar mobility to each other, either deposit eggs singly *or* in batches (Stamp, 1980). *Batus philenor* (Papilionidae) lays small egg batches on each of several *Aristolochia* leaves. The fast-flying skippers also lay single eggs, as expected from ISC, but so do many other butterflies (Sillén-Tullberg, 1988). *Trichoplusia ni* (Section **5.2.1.4(m)**) lays many eggs one at a time on adjacent plants (Shorey *et al*., 1962). More robust noctuid moths typically lay several egg batches in separate patches. Hawk moths are medium to large, always fast flying and have typically widespread egg distribution. Their eggs are placed in ones and twos (not liberally scattered as in swift moths) on small, isolated plants sufficient for the needs of only a few larvae. Thus, 12 of the 17 British species oviposit on vines and herbs (South, 1920/1923). The hawk moth *Celerio galii* is an extreme example. Hundreds of eggs are placed in ones and twos on little patches of bedstraw. In Costa Rica 82 of the 101 hawk moths favour species-specific shrubs, vines and herbs (Janzen, 1984) laying 'one or a few eggs' in each patch. Since females can mature several hundred eggs, the progeny is distributed over numerous patches, although if these are big several eggs may be deposited, as in *Pseudosphinx tetrio*. Hawk moths, being 'hot blooded' (Heinrich, 1993) are less affected by bad weather, than are, for example, butterflies (Section **10.2.5.3**). The mullein shark, a relatively large and fast-flying British noctuid species, has a similar egg distribution to most hawk moths.

Apart from locating potential food items, females often select suitable ones (Myers, 1985), the first part of the PPL. So egg distribution comprises two behaviours, food finding and food selection. Scattered egg distributions preclude gregarious larval behaviour. If eggs are laid in batches, when they could be laid singly, we suspect sibling co-operation to ensue. While such distributions are expected to entail a metabolic cost, this is defrayed in HISC insects by their enhanced ability to seek fuel, as well as scattered oviposition sites. So while resource distribution determines *potential distribution*, egg distribution defines the achieved spatial distribution of each generation, that part of redistribution and resource finding under maternal control (Section **12.2.4.1**) and the primary component of population dynamics.

Apart from spatial relationships, temporal ones also impact insect reproduction (Sections **5.2.1.4(g)** and **6.2.1.2(c)**); as when asynchrony between eclosion and the presence of adequate food occurs (phenological asynchrony; Watt and Woiwod, 1999). This applies to both plant food and to parasitoid hosts. Asynchrony can apply to oviposition itself or to egg hatch. But there may be a conflict of genetic interest between parents and offspring (Bonal *et al*., 2010). For the weevil *Curculio elephas* in Spain, egg laying occurs within and outside the optimal period for larval growth. Females effectively add less favoured offspring to those experiencing the best conditions. Also, several chalcidoid parasitoids of the horse chestnut leaf miner are poorly synchronized with their host's life cycle (Grabenweger and Lethmeyer, 1999). Finally, size may affect the reproductive performance of males. Thus, in *Epirrita* males below a mass of ~50 mg have less capacity to inseminate females, small size being mainly a result of poor diet, in turn caused by induced resistance in their *Betula* food plant (Haukioja, 1980). Male size also affects mating tactics in some swarming midges, some tenebrionid beetles and the Californian oak moth (Section **10.2.5.1**).

10.2.5.3 Reproduction: Physical factors: Temperature and insolation

Temperature variously affects MPF through juvenile development (Sections **10.2.2.2** and **10.2.5.2**), physiology, final size and often interacts with food. In *Pieris rapae* the former interaction affects pupal mass and in turn AF. From 15°C to 25°C the rate of larval development increases about threefold, but pupal mass is much less at the higher temperatures (Gilbert, 1984). Larvae fed on Chinese cabbage, however, are less affected by temperature than those fed on kale. Overall, the mean pupal mass of Japanese *P. rapae* at 25°C varies from 98–193 mg on several different food plants (Ohsaki and Sato, 1994). AF increases from 200 to 700 eggs/female as pupal mass doubles from 120 mg to 240 mg (Gilbert, 1984), it more than trebles as body mass doubles, as in *Sceliphron* (Section **10.2.5.2**) and *Epirrita* (Haukioja and Neuvonen, 1985). In this moth, while the relationship between pupal mass and the number of eggs developed is significant ($P < 0.0001$), other external factors come into play (Heisswolf *et al*., 2009). A close link to size exists in the adelgid bug (Section **4.3.3**) *Pineus pinifoliae*, the smallest females laying ~15 eggs and the largest ones ~150 (Sopow and Quiring, 1998), who say that other 'environmental factors' may be involved! For *Epirrita*, while there is much spread, pupal mass declines as the sum of day degrees increases, and high parental densities reduce egg numbers in the adult offspring.

Temperature also affects reproduction by adult *behaviour* as well as physiology. We separate here effects at mating, and in train on fertility, from those that occur afterwards. In three *Drosophila* spp., high temperature reduces mating frequency (Fasolo and Krebs, 2004) and hence fertility in the population. In *D. mojavensis* mating frequency is normal at 25°C but reduces linearly to zero at 37°C. *Below* the threshold temperature for flight, many active insects, as in Odonata, Lepidoptera and Diptera, cannot meet and mate. *Papilio machaon* produced a high percentage (~14%) of infertile eggs in a period of bad weather (Dempster *et al*., 1976). Both sexes, but especially males, are often sterile at low temperatures. In Vancouver, no *Trichoplusia ni* females, having survived 10°C for three weeks as pupae, laid any eggs (Caron and Myers, 2008).

In species in which eggs develop in the adults, the rate at which they do so depends on MR, a physiological effect. MR depends on temperature, and in females that bask, on insolation. In *Encarsia formosa* while the rate of oogenesis depends on temperature during the day, females develop further eggs during the night, which are available to lay next morning (van Vianen and van Lenteren, 1986). *Pararge aegeria* (Satyridae) matures eggs faster on warmer nights, giving them the opportunity to lay more eggs on the next suitable day (Berger *et al*., 2008). House flies and blow flies basking in the sun are a too-familiar sight: females so engaged raise their body temperature 'for free', and hence speed up egg development. In the temperate grasshopper *Chorthippus brunneus*, laboratory work shows that AF is low without a source of radiant heat (Begon, 1983). As with growth, the distribution of fecundity with temperature is skewed, the optimum being nearer the maximum than the minimum (Karlsson and Wiklund, 2005). But constant laboratory temperatures may not reflect field conditions. *Therioaphis maculata* (Section **5.3.1.2(g)**) produces eggs from 8–32°C when temperatures fluctuate as in the field, but only between 15°C and 30°C when they are constant (Messenger, 1964b).

Temperature also affects egg distribution (Section **10.2.4.7**), namely a *behavioural* influence. In all cases the egg distribution characteristic of the species is possible only if temperature is above a threshold. This is low for flightless moths and heterothermic moths, much higher for butterflies, parasitic wasps and flies. Assuming adequate temperature, the extent of egg distribution depends on female ISC, whether this is limited (Tipulidae, many Lymantriidae) or advanced (Sphingidae, big butterflies, large Noctuidae and Calliphoridae), and of course on the density and apparency of oviposition sites. Even species that do not leave their natal patch need the temperature to be above this level for oviposition (25°C for the louse *Pediculus*). So there is a sequence of effects between temperature, egg distribution and AF via movement (Sections **10.2.4.4** and **10.2.5.2**).

Continuing bad weather, little sunshine and low temperatures curtail AF of most insects. This often happens in temperate spring if temperatures remain below the activity threshold. It is not just that sunshine raises ambient temperature. On partly cloudy days many more insects fly during sunny spells, although shade temperature varies but little. Insolation contains both radiant heat and radiant light, so greater light intensity may allow them better visual discrimination. In several diurnal groups, like butterflies, wasps and flies, sunlight induces flight, and hence their chance of finding mates and laying eggs. In *Anthocharis* (Section **9.1**), AF is correlated with hours of sunshine (Courtney and Duggan, 1983), few eggs being laid on cloudy days (Dempster, 1992). In spring 2012 and 2017 in southern England 3-week periods of cold weather almost totally inhibited their flight and so feeding (Freeman, personal observation). They could not lay eggs and many probably died without breeding. In such cold springs, having, say, six warm days instead of three may well double AF. The great abundance of its food plants, let alone competition (Section **10.1.2**), being irrelevant to its dynamics. Then, in *Limenitis camilla*, egg counts, relative to the numbers of adults flying, were directly related to mean daily maximum temperature and to hours of sunshine (Pollard, 1979). Also in Britain, the hours of bright sunshine received regionally are a likely determinant of butterfly diversity (Turner, J.R.G. *et al*., 1987). In sub-arctic *Epirrita*, the numbers of eggs laid per night are related linearly to temperature, although a few are laid even when it is sub-zero (Tammaru *et al*., 1996). These effects show the dominant influence of weather in determining insect numbers and diversity in such situations. In the tropics torrential rains and low temperatures can curtail flight and inhibit oviposition (Section **10.2.5.4**). But some species, like *Anastraepha obliqua* (Section **6.3.1.1(n)**), do not oviposit when temperatures are too high (Aluja, 1994). In the aphid *Toxoptera citricida*, total nymphal production falls steadily from ~50 at 10°C to ~10 at 28°C. Apart from temperature effects on reproduction within a generation, in many species mean temperature determines the number of generations/year. Cool years have fewer generations (Section **10.2.2.2**).

10.2.5.4 Reproduction: Physical factors: Precipitation and moisture

Rain may limit breeding even though temperature is favourable. In the Caribbean, several solitary wasps are so limited (Freeman and Taffe, 1974; Freeman and Jayasingh, 1975b). In Trinidad, *Trypoxylon palliditarse* lays fewer eggs the higher the mean rainfall (Fig. 10.23). Persistent rain makes it time consuming for females to find dry nesting sites, and, having started to lay, increases the time needed for provisioning (Freeman, 1981a). But in *Heliothis zea* high humidity *after* rainfall induces faster oviposition and drought results in reduced AF. In *Sceliphron*, Jamaican field data give a mean duration of reproduction of 38 days in good weather (sunshine, few showers), while during continuing drought it is only 28 days. Mean AF was 11.3 ± 2.6 in good weather, only 7.5 ± 2.0 (95% CI, $P < 0.05$) in drought (Freeman, 1980). These wasps migrate to areas of higher altitude and MAP during drought, while their progeny may fly to the drier lowlands when it gets too wet (Freeman, 1977; Section **10.2.1**).

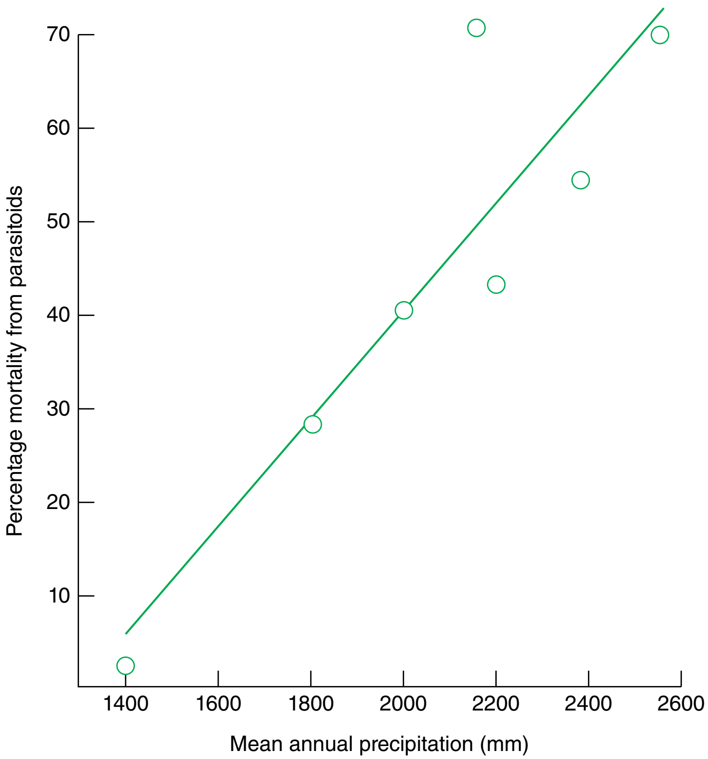


Fig. 10.23. Achieved field fecundity in *Trypoxylon palliditarse* in relation to rainfall. Adapted from Freeman, B.E. (1981a) The dynamics in Trinidad of *Trypoxylon palliditarse* Saussure: a Thompsonian population? *Journal of Animal Ecology* 50, 563–572. Fig. 2.

Indeed, temperature and humidity may act together on fecundity, a combination that has been studied in several pests of stored products. In two contrasted pests, the warehouse moth and the tobacco beetle, one can construct contours of equal fecundity for various experimental combinations of these factors (Fig. 10.24). The moth requires lower temperatures and slightly moister conditions than does the beetle. The figure shows that dry, cool storage discourages the population growth of such pests by reducing their AF.

10.2.5.5 Reproduction: Physical factors: Light

While incident light has little effect on fecundity *per se,* it may influence other aspects of reproduction. Insects are active either during the day or the night, constraining their reproductive activities, and high incident light is associated with elevated temperature. Of course, the activity of most moths, and hence mating and oviposition, is nocturnal (Section **10.2.3.5**). In *Ostrinia nubilalis*, mating is induced by fading light and falling temperature (Brindley *et al.*, 1975). Mating swarms of Nematocera often occur at dawn and dusk, nubile females being attracted to the movement and sound of the male swarm. Light also affects microhabitat selection and egg laying. The wasps *Pachodynerus nasidens* and *Trypoxylon texense* do not occupy trap nests in open fields, only in shaded situations (Jayasingh and Freeman, 1977). The leaf-mining agromyzid fly, *Liriomyza*, lays eggs only in shaded leaves of its food plant, so avoiding high insolation and temperatures for its larvae (Freeman and Smith, 1990). But some Costa Rican Chrysomelidae tend to avoid shade (Risch, 1981). Since many such beetles have metallic colours (Section **10.2.4.2**), we suspect they are sun loving when breeding. In the long term, reducing annual photoperiod induces production of the sexual forms of many aphids (Lees, 1966). Laboratory studies on

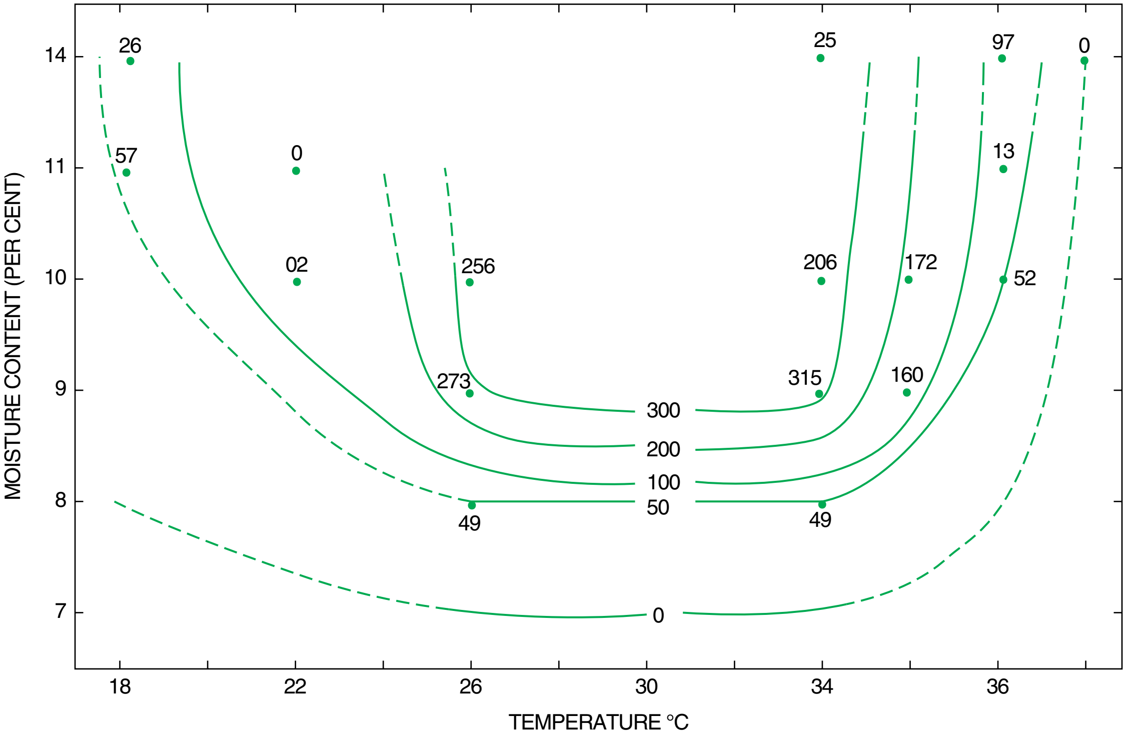


Fig. 10.24. Lines of equal fecundity in the stored-products beetle *Rhyzopertha dominica* according to temperature and moisture. From: Andrewartha and Birch (1954) *The Distribution and Abundance of Animals*. Chicago University Press, Fig. 7.37, p. 282. Reproduced with permission.

the parasitic cynipoid wasp *Leptopilina heterotoma,* show that reducing photoperiod induces greater reproductive effort (Roitberg *et al*., 1993). But a similar effect occurs with reduced atmospheric pressure, to wit, a mechanical factor. It may be that these increased efforts stem from the wasp's detecting impending hazards, the former indicating approaching autumn and the latter impending storms.

Reflected light often allows SMRS (Section **10.1**) at a distance, naturally mainly in diurnal insects. Many butterflies are sexually dimorphic. Thus only the males of *Anthocharis cardamines* (Section **9.1**) have orange-tipped wings, and in many yellowish pierid butterflies, such as *Anteos, Eurema* and *Pheobis*, the males are brighter than the females. In Jamaica *Papilio thersites* males are mainly yellow, the females mainly brown. The swarming males of *Argyra diaphana* (Dolichopodidae) in dim woodland light, display conspicuous silver abdominal patches (Colyer and Hammond, 1951), thus signalling their presence to females. Of course, chemical recognition by smell and touch will also generally come into play.

Reflected light is often used to find oviposition sites. The weevil *Exophthalmus* (Section **3.2.2.1**(**b**)), some *Papilio* spp. and the leaf miner *Phyllocnistis* (Section **5.2.2.1**(**c**)) are attracted to the light green flushes of citrus foliage. Ovipositing *Simulium* and mosquitoes are attracted to reflective surfaces, by which they find water bodies in nature. Dragonflies are often seen vainly attempting to oviposit on polished cars. In addition, the butterfly *Battus philenor* recognizes the *Aristolochia* food for its larvae by leaf shape (Rausher, 1978).

10.2.5.6 Reproduction: Biotic factors: Conspecific organisms and population density

This is another primary effect of density (Section **10.1**), one relating to mating frequency. Its distribution includes unmated, singly and multiply mated females. In sparse populations of short-lived adults with poor ISC, such as in midges, mating with the first male encountered may be as good as it gets. But an increasing proportion of females fails to find a mate as density falls, an Allee effect (Section **10.2.5.1**), and those that do so after a relatively long period, have less time to oviposit. Of course, unmated females in most groups remain sterile. But at higher densities and/or in long-lived species, polyandry becomes frequent. Thus, as in parent/offspring conflict (Trivers, 1974), sexual conflict may occur as the evolutionary aims of the two sexes differ (Arnqvist and Nilsson, 2000; Gwynne, 2008). Males try to sire as many offspring as possible, females try to discriminate males that enhance their fitness (Williams, 1966; Thornhill, 1976). Multiply mated females have more diverse progeny (Svärd and Wiklund, 1988), which will spread risk (den Boer, 1968) and reduce any sibling competition. Field paternity in offspring can be estimated with micro-satellite DNA markers (Estoup *et al*., 1995; Song *et al*., 2007). Allee effects may reduce growth, survival and fertility, so there will be multiple outcomes, including genetic ones (Parker, 1992; Hardy, 1994; Berec *et al*., 2006; Duplouy and Hanski, 2015).

Males try to ensure they fertilize all their mate's eggs. This should be critical at high density, where mating frequency can be high. Even so, in Colias butterflies, all the progeny may be sired by a female's last mate (Boggs and Watt, 1981, in Watt *et al*., 2003). Nuptial gifts attempt to assure paternity, often enhance joint reproductive output, so being a form of co-operation, and may protect the offspring (Lamunyon, 1997). Clearly, there are two routes to enhance such female nutrition: seminal and oral (Gwynne, 2008). But as expected, males may use them to try to eliminate sperm competition from other males (Parker, 1970; Thornhill, 1976; Trivers, 1985). In some groups including mosquitoes, male accessory glands produce proteins inhibiting further mating (Craig, 1967; Gillott, 2003). Some *Pieris* spp. males, after transferring a large spermatophore (see below), cloak the female in anti-aphrodisiac, so protecting their investment (Andersson *et al*., 2003). This wears off in a few days and females often take the opportunity to mate again. Conversely, multiple matings take place in quick succession in honey bee queens, and may well enhance AF. Polyandry occurs in *Bombus* spp. (Estoup *et al*., 1995), some Parasitica (Freeman and Ittyeipe, 1993) and Lepidoptera, where there is much variation (Oberhauser, 1997). Here, male investment is common as there is often nutrient transfer in spermatophores (Boggs and Gilbert, 1979). These lipoprotein packets occur sporadically from Diplura to Diptera, but notably in Neuroptera and Mecoptera (Thornhill, 1976). They may have evolved from an early mode of sperm transfer (Alexander, 1964), shielding the sperm from desiccation. They are also frequent in Orthoptera (Gwynne, 2008), where male investment may be considerable (Simmons and Thomas, 2004). In *Ephippus* (Tettigoniidae), the spermatophore is ~25% of the male's mass (Thornhill, 1976). Unsurprisingly, in *Melitaea cinxia* (Section **10.2.2.5**) small males produce small spermatophores (Duplouy and Hanski, 2015).

But much enigmatic mating behaviour exists. *Danaus plexippus* females mate up to eight times and large spermatophores are transferred. Oddly, laboratory trials show that polyandrous females have similar longevity and AF to once-mated ones (Svärd and Wiklund, 1988). While spermatophores are large they are 85% water, but may postpone further mating. So for males, paternity rather than investment seems key. For females, in addition to increased variability of the progeny, acquiescence to copulation may be a safer option than refusal since the act can be brutal. In several delphacid genera such as *Ribautodelphax*, there are both diploid and triploid females (den Bieman, 1988). Sexuality in diploids is normal, but triploid females must mate before they can lay eggs, although males contribute nothing genetically to the offspring! One suspects that males are being duped into copulation for nutrients in their semen, but the reproductive output of diploid and triploid females is similar (P >0.10). Females mate up to three times in *Heliconius hecale* (Nymphalidae) and *Melittobia*. In *Trichoplusia ni*, triply mated females are more than twice as fecund as singly mated ones (Shorey, 1963). Multiply mated *Nilaparvata* are more fecund than once-mated ones (Oh, 1979, in Denno and Roderick, 1990). But in *Busseola* (Section **4.4.1.1**(**c**)) polyandry has no effects on fecundity or fertility (Unnithan and Paye, 1990), although delayed mating can reduce both. In *Utetheisa ornatrix*, male and female moths contribute an alkaloid from their food plants to defend the eggs (Dussourd *et al*., 1988; Lamunyon, 1997). Age in both sexes, among other factors including host size, may affect the sex ratio of the progeny in parasitic Hymenoptera (Waage, 1986). When seeking to unravel the demographic outcomes of polyandry we must be certain that females that have the propensity for this behaviour do not already have the correlates in question.

While competition (Section **9.8**), either intraspecific or interspecific, is not the all-pervading influence it was once thought to be (Shorrocks *et al*., 1984; Walter, 2003), there are still many cases in pest insects in which it has a marked effect in reducing individual AF. This is often so in pests occurring at high densities, which are common in the sense that they use up much of their resources. For intraspecific competition, bark beetles (Section **4.2.1.2(h)**) provide a clear case in point. When a forest tree is heavily infested their brood galleries cross each other, giving rise to competition for the space to lay eggs, and *leading to* reduced AF (Fig. 10.25). In turn, such competition may *lead to* diminished survival of the progeny as these compete in a similar way for space. In clover seed weevils ovipositing females avoid pods already used by another female (Section **10.2.4.7**; Freeman, 1967a). While this must waste time it is probably minor since females have a limited number of eggs they can lay per day and other suitable clover florets are legion. Then, parasitoid females sometimes reject hosts that are already parasitized either by themselves or by other females (but see Section **8.2.2.5**). Also, in several butterfly species ovipositing females avoid leaves already bearing eggs, or are deterred by an ODP left by an earlier female (Section **10.2.4.7**). A similar situation is often found in the ovipository preferences of leaf miners.

10.2.5.7 Reproduction: Biotic factors: Other organisms: Enemies

Parasitoids usually attack only the juvenile stages of their victims, often causing their demise (hence *parasitoid* not *parasite:* Section **8.2.2.1**). However,

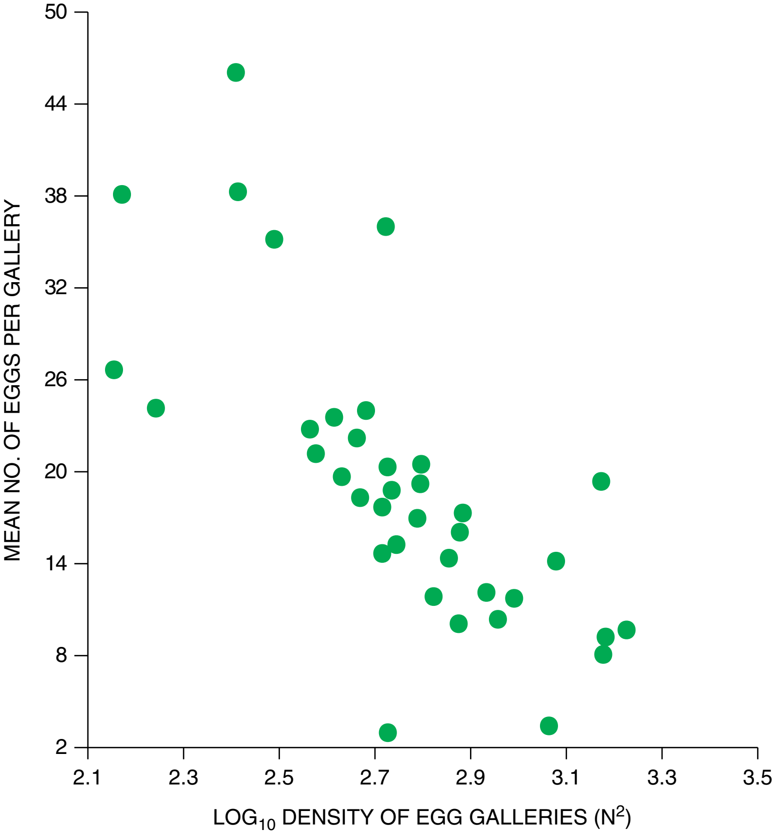


Fig. 10.25. Reduced fecundity in bark beetles caused by competition for space. Adapted from: Garraway, E. and Freeman, B.E. (1990) The population dynamics of *Ips grandicollis* (Eichhoff) (Coleoptera: Scolytidae) in Jamaica. *The Canadian Entomologist* 122, 217–227. Fig. 1, p. 223. Reproduced with permission.

many cases are known, and certainly more exist, in which hosts encapsulate parasitoid larvae or otherwise kill them and hence survive to adulthood, both parties survive or both die (Flanders, 1942; Richards and Waloff, 1948; Armstrong, 1958; Puttler, 1967; Parker and Pinnell, 1973; Stoltz and Vinson, 1979; Edson *et al*., 1981; DeVries, 1984; Harcourt, 1990; Godfray, 1994; Strand and Pech, 1995; Singer and Stireman, 2003; Danyk *et al*., 2005a and b; Schmid-Hempel, 2005; Section **10.2.3.8**). One expects females surviving such a battle to have reduced AF. This is borne out in a suite of grasshoppers attacked by nemestrinid flies in prairie (Laws and Joern, 2012), and by the bug *Eurygaster* by tachinid flies (Iranipour *et al*., 2011). Such outcomes are likely in *Grammia* and *Pieris* (Section **10.2.3.8**), but one must carefully separate the negative effects of food plants from those of parasitoids. In *Platyprepia virginalis* (Arctiidae), parasitism by *Thelairia americana* (Tachinidae) causes a change in food preference in these larvae from lupine to hemlock (*Conium*) (Karban and English-Loeb, 1997). They then survive better while subsequent AF is unaffected. Occasionally, even larval hosts damage their adult parasitoids as in fifth instar *Trichoplusia ni* and the tachinid fly *Compsilura concinnata* (Caron *et al*., 2010). An open question is: Do parasitoids kill their hyperparasitoids?

There are several examples of *adult* insects, especially coccinellid beetles and weevils, being attacked by parasitoids, gradually terminating their egg laying. For example, *Microctonus* (Braconidae), a genus attacking the adults of several beetle genera (Section **6.2.1.2(a)**), affects *Apion dichroum* and *Hypera postica*. Parasitoids in *Cryptoxilos* and *Cosmophorus* (Braconidae), and *Amblymerus* and *Tomicobia* (Pteromalidae) attack adult bark beetles (Bushing, 1965). When female *Nezara* are parasitized by the tachinid fly *Trichopoda* (Section **6.3.2.1(a)**), they suffer reduced AF and premature death, an effect also found in *Zonocerus* grasshoppers and Colorado beetles. Similarly, *Coleomegilla maculata* females parasitized by *Perilitus coccinellae* continue to lay eggs until just before they die (Smith, 1960; Section **8.2.2.4(e)**). In addition, conopid flies attack *Bombus* workers (Goulson, 2003). DeVries (1979) found fly maggots in a morpho butterfly, and I once discovered an adult female *Tipula oleracea* with a maggot in its abdomen, but failed to rear it.

Predators can kill adult insects before, during or after egg laying. The first is part of *pre-reproductive adult mortality*. The second abruptly reduces potential fecundity to AF and the third is of small interest to ecologists. But the physical damage caused by unsuccessful predation may reduce AF. In some mosquito species even the presence of enemies, such as *Toxorhynchites*, *Notonecta* and fishes, deters oviposition. Indeed, several non-insect enemies can reduce reproduction of their victims, even if they are not lethal (Section **10.2.3.9**). Sublethal attacks by parasitic nematodes are known or suspected to decrease AF. These nematodes include *Steinernema* on soil insects, *Bursaphelenchus* on cerambycid beetles and *Heterorhabditis* on bark beetles. The *Rickettsia*-like bacterium *Wolbachia*, however, has more subtle effects (Werren, 1997; Werren and Windsor, 2000; Section **10.2.3.9**), causing cytoplasmic incompatibility, feminization and selective killing of genetic males. According to its severity, this naturally reduces reproductive output. Type A and B bacterial strains exist, type A being frequent in the Hymenoptera, type B in the Lepidoptera.

10.2.5.8 A summary of density effects

Putting the influences of the physical environment to one side, the effects of population density on the rate of increase of a bounded population can be summarized in an insightful diagram by Murray (1994; Fig. 10.26). For both birth rate (*b*) and death rate (*d*) there is a lower critical density, below which *b* falls and *d* rises. This is due to the Allee effect (Section **10.2.2.4**). Then there may be a range

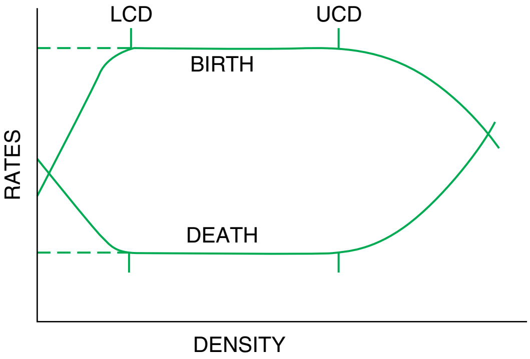


Fig. 10.26. The effects of birth and death rates in a bounded population. From Murray, B.G. (1994) On density dependence. *Oikos* 69, 520–523. Fig. 2, p. 522.

of density in which neither *b* nor *d* is much affected, but above an upper critical density *b* again declines and *d* again rises.

10.3 Conclusions

The above is a condensed account of that part of insect ecology that is basic to, but only touches on, the big picture of insect population dynamics itself. We have been concerned almost exclusively with the ecology of single insect species, mentioning communities and the recycling of energy and elements only as a background. The subject matter here provides answers to Andrewartha and Birch's first question 'Why does the species under study occupy so much of the Earth's surface and no more?', and supplies *components* of the answers to their questions on its dynamics. Thus, a variety of factors both physical and biotic, such as adverse hygrothermal conditions and reduced quantity and quality of food, slow the growth and development of individuals. This results in a longer generation length of the population they comprise. In extreme cases, and often where the species is close to the limits of its distribution, bad weather can cause the life cycle to be truncated, that is, many individuals simply fail to reach the stage adapted for the harsh season (Section **10.2.2.2**). Such a component can enter into the equations of population growth as extrinsic factors (Turchin, 2003). The data given also assist in devising methods of economic control of pest species.

Students should now appreciate that the diverse ecologies of different species can be reduced to rational components. In other textbooks, different ways of classifying the material may be adopted: essentially the same material is looked at in different perspectives, which adds fullness to our view of nature. Science is not dogma. Although in time the best systems gain consensus, the majority view is not always correct. Neither is science democracy. And even so, there is not necessarily *one* best system: multiple perspectives enhance understanding. Fresh ways of looking at old or new data are always useful. Apart from the biological basis of pest control, there are other areas of human endeavour with which biological knowledge has to be integrated if pests are to be controlled in practice, as well as in theory (Van Driesche and Bellows, 1996; Pedigo, 1996, 2002; Dent, 2000; Thacker, 2002; van Emden and Peakall, 1996; van Emden and Service, 2004). They are comprised in the term 'integrated pest management' (Section **13.3**), and include sampling and forecasting of pest outbreaks, advances in the design and use of agricultural machinery, modification and timing of husbandry, the application of insecticides and other chemicals, governmental legislation and quarantine procedures, and of course managerial skills. These areas will be dealt with in the final chapter. But now we consider the heart of the problem: our grasp of insect population dynamics, without which there can be no deep understanding of the control of pest insects (Berryman, 1991b; Walter, 2003). Populations attack our crops, although comprised of variable individuals, as we have seen.

Finally, returning to the species-abundance distribution (Section **9.4**), nearly all work on insect populations has been done on herbivores with high densities, giving a very biased view of the subject (Section **12.1**). Far more work must be carried out on rare species, simply to redress this bias (Jayasingh and Freeman, 1980; Cappuccino and Kareiva, 1985; Hawkins *et al*., 1997) and especially on predators, parasitoids, hyperparasitoids and detritivores.

11 The Dynamics of Insect Numbers 1: History, Classical Theories, Time Series, Life Tables, Models

11.1 A Brief History of Population Dynamics and Evolution

11.1.1 General introduction

Apart from some formative inputs by Darwin (1859) and Spencer (1864), economic entomologists first researched the natural control of animal numbers. They sought to explain how insect populations varied in size from year to year and from place to place, but pest outbreaks were of prime concern. Only with Thompson and Nicholson (below) did attention centre on wider aspects of the *natural control of animal populations*. Then, as ecologists became aware of the pressing need to conserve endangered species, they began to examine populations at the other end of the numerical scale. Ultimately, the anthropocentric view of the prime importance of mammals and birds gained weight, which we will not add to.

Apart from the authors of the *Classical Theories* below, L.O. Howard and W.F. Fiske (Fig. 11.1) were significant early workers. But those using insects in *population genetical* studies, especially Dobzhansky and Ford, made contributions widening our view. Their names and the dates they worked help one to appreciate the subject's development. While noise in the system exists, we see how new ideas built on old ones (Price, P.W., 1997). History of science is essential for breadth of understanding and for guiding future action (Carr, 1987), although past gains are often forgotten (Taylor, 1984) in the rush to publish. History is a *temporal* aspect of human endeavour, *geography* its spatial counterpart (Section **2.1**). Those with scant knowledge of their subject's history often try to re-invent the wheel (Oksanen, 1991). A glaring case is Murrell *et al.*'s (2002) evaluation of insect redistribution without mention of the detailed work by R.A.J. Taylor (1978, 1980), even though it appears in major journals. Ignorance of a discipline's history is at least as bad as ignorance of recent developments, especially since definitions are lost. See the cases of 'abundance' (Section **9.2**) and 'competition' (Section **9.8**). Merely using a search engine for key words is not enough, errors of omission are self-perpetuating. Even mistakes are worth noting as they assist clarification (Popper, 1989), and could easily be made again. So, sometimes I include a little history. Also note that history in biology comes in two distinct areas: (i) the history of philosophy and science; and (ii) palaeontological history as an aid to understanding ecology, evolution and other areas of biology in the present.

11.1.2 Historical perspective

Aristotle pondered the origin and decline of locust and mouse plagues, but not until the Renaissance did thinkers begin to inquire into population processes. In general, progress in Europe was stifled by the belief that plagues resulted from God's wrath against the sinful, as in Genesis. Graunt (1662) included the effects of sex ratio and age distribution on human birth and death rates, estimating London's population would double in the next 64 years. But the Great Plague grimly reaped ~20% of Graunt's initial population (Section **7.2.2.2(b)**). Later during the Enlightenment, Pierre Louis Maupertuis (Fig. 11.2) developed the concept of a population with *variable individuals*, and in 1760 his colleague Leonhard Euler wrote a growth equation for an age-structured population. Malthus's (1798) 'Essay on Population', directed at understanding the expanding human population during the Industrial Revolution, had a germinal effect on evolutionary theory. He employed an idea from Nicolas de Condorcet in his 'perfectibility of society' (Rothschild, 2001), that while such population increase was exponential, the food resources needed to feed it could be increased only in a linear manner. Starvation of the work force was just down the road!

Fig. 11.1. L.O. Howard who, with W.F. Fiske, made formative advances in insect population studies in the early twentieth century. Source: Wikimedia Commons.

Fig. 11.2. Pierre-Louis Maupertuis who, in the eighteenth century, first promoted the rational study of inheritance. Source: Wikimedia Commons.

Malthus's (a name derived from 'malt house', indicating a family concern in brewing not an exotic origin) idea was taken up as a component of *natural selection* and *survival of the fittest*. The latter phrase derives from Spencer (Costa, 2013) and encapsulates the idea that natural selection and population dynamics are interwoven (Section **11.2.1**). But there were proponents of natural selection long before Charles Darwin, including his fabulous grandfather, the polymath Erasmus Darwin (Fig. 11.3; Section **9.10**). The record of Anaximander's original discovery of organic evolution (about 550 BC) having been lost, in 1770 Erasmus startled the local clergy by promoting the process of evolution on his family crest, which bore the motto '*E conchis omnia*' (everything from shells). The much-maligned Jean Baptiste Lamarck then developed the concept in France. But long before Charles returned from his travels on the Beagle, William Wells used natural selection to explain human skin colour (Green, 1957). At the Royal Society in 1813 he noted: 'What is done by art' (artificial selection during domestication) 'seems to be done with equal efficacy, though more slowly, by nature …' (Eiseley, 1961). Edward Blyth used the concept to explain why skylark chick plumage matched the soil colour on which their parents nested. While Blyth wrote to Darwin, he had not come to think that natural selection could lead to speciation (Dobzhansky, 1959). Not so with Patrick Matthew who wrote after noting natural selection among forest trees, that the progeny of the same parents, 'under great difference of circumstance, might in several generations become distinct species incapable of co-reproduction'. But unlike Darwin they made little effort to develop the idea (Mayr, 1982). As Russell (1961) puts it, however, 'Beginnings are apt to be crude, but their originality should not be overlooked …'.

Fig. 11.3. Erasmus Darwin, grandfather of Charles Darwin, rediscovered the principle of organic evolution in the late eighteenth century. Anaximander, the Milesian philosopher, originally promoted the concept in the fifth century BC after discovering fossil fishes in rocks high above sea level. Orogenesis being unknown, the observation is congruent with the notion of evolution of terrestrial animals (reptiles, mammals) with like fishes, backbones, in response to a drying world. Source: Wikimedia Commons.

Then in 1838 came the advance noted above. The Dutchman P. F. Verhulst (1838), probably with inputs from his mentor Quetelet, produced a significant and longstanding deductive model in population biology. He used two ideas: (i) population growth (r) was exponential; but (ii) there was a limit (k or K) to population size (N) due to a *constancy* of resource input to the system. This limit is the '*carrying capacity*' and was usually held to be fixed in *natural* systems. His equation may be written as:

$$dN/dt = rN(1-N/K)$$

an example of bounded population growth. The per-capita growth rate $r(1 - N/K)$ depends on the number of individuals in the population, growth rate being a function of its size. This is positive if $N < K$, zero if $N = K$ and negative if $N > K$, and hence leads to a stable equilibrium where $N = K$. The integral form defines a sigmoid curve of population growth to the asymptote K. While this concept has had an enduring place in population ecology (Section **11.5.2.1**), we will see that to achieve realism it must be related to fluctuations in resource supply and to levels of resource space (Section **12.2**). In reality these are never constant.

Apart from the inputs above, Darwin's mind was probably conditioned to the concept of evolution by reading his grandfather's work *Zoonomia* (1794–1796) (King-Hele, 1999). He and Alfred Russell Wallace collaborated to develop the theory of the survival of the fittest. It implies, relative to existing conditions, that *conspecific individuals are unequal* (Burt, 1995), that is, *they vary*. As F. Scott Fitzgerald (1926) put it: '… the fundamental decencies [are] parcelled out unequally at birth'. This inequality is due to inheritance and to environmental influences during development, a duality popularly referred to as *nature* and *nurture* (Section **9.6**). Evolution involves the dynamics of populations: the '*struggle for existence*', so only a few favoured and fortunate individuals out of many survive to reproduce. But were there no *heritable* components to inequality, selection could not change the intrinsic nature of population through time. Remarkably, Erasmus Darwin (1800) pointed out this constraint in *Phytologia*, an imperative confirmed by his grandson (Darwin, 1859) and by, for example, Fisher (1930) and Endler (1986).

In 1751 Maupertuis outlined a 'genetic' theory hinting at dominant and recessive *particulate* factors derived from both parents (Hampson, 1990). Much later Charles Naudin upheld the particulate nature of inheritance. But in Charles Darwin's time the mechanism was thought generally to be blending (Wright, 1982a). Blending is problematic since it leads inexorably to loss of variability. Only Abbé Gregor Mendel and a few colleagues in Brno knew evolution's true particulate nature. It remained so until Correns, de Vries and Tschermak unearthed Abbé's 1866 work (Huxley, 1942), bringing it to light in 1900, when the good Abbé was unable to reap his due glory on Earth. Not to mention Maupertuis! Three aspects of the struggle for existence are significant for economic entomology today. First, most individuals die before they can reproduce (Section **10.2.3**). Second, obversely, in any pest population a few individuals will be hard to kill. Thus, in *Myzus persicae* some strains show 4000-fold more resistance to organophosphates than others (Section **13.2.3.4**), an extreme case of the power of evolution. Third, insects and their biotic environments evolve, often rapidly.

Darwin (1859) promoted competition (Sections **9.8**, **10.2.3.7** and **10.2.3.10**) as a major force in the struggle for survival, both within species and between them, especially between related ones. He says:

> As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between species of distinct genera.

Competition was a major biotic interaction with far-reaching effects. While many workers hold this view today, it depends mainly on one's definition (Section **9.8**). Darwin was a retiring man, often unwell, but fortunately for human enlightenment T.H. Huxley, son of a schoolteacher, appeared as a Luther-like proponent of Darwinism (Desmond, 1994). Wallace (1888), the forgotten man of evolution, went on to describe how speciation might occur (although lacking knowledge of genetics; Section **9.10**), a process signally absent from '*The Origin*' (Orr, 1996).

The early years of the new century were heady times for biology. First, Mendel's particulate inheritance was verified, T.H. Morgan (Fig. 11.4) set to work on the genetics of *Drosophila* and in 1908 G.H. Hardy, the illustrious Cambridge mathematician, in an apologetic little note applying binomial theory to the new science, set population genetics in its train (Hardy, 1908). Wallace, Poulton and Jordan together developed the concept of species (Mallet, 2004). Here, mutual fertility was the criterion and evolutionary change possible. Recall that Linnaean species, while variable, are fixed and immutable (Section **9.10**). Then Bateson (1909), with great insight, suggested more fully how speciation could occur by the *evolution* of sterile hybrids. The evolution of sterility, whether of hybrids or of worker castes, is itself a thorny problem (Section **9.10**). Bateson, and later Dobzhansky (1937) and Muller (1942) solved this impasse by showing that hybrid sterility could be caused by interacting sets of complementary genes coming together in a *novel genetic environment* (Sections **9.10** and **11.2.3.1**), while Mayr (1942) further developed the biological species concept.

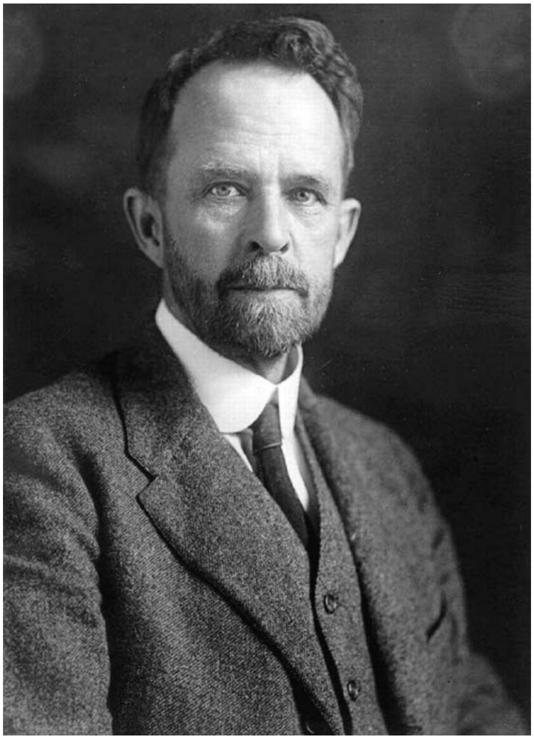


Fig. 11.4. T.H. Morgan, using *Drosophila*, massively promoted experimental genetics. Source: Wikimedia Commons.

Other key developments in ecology, relating to population theory, took place in North America in 1911, when L.O. Howard and W.F. Fiske (above) were studying parasitism in forest moths. With great insight they suggested that (extrinsic) mortality factors were of two sorts. First, there were those like extremes of weather (frost, flood and drought) that killed, *according to their severity*, a proportion of an insect population independent of its density. These they called *catastrophic factors*, although this term over-emphasizes their true nature. Second, the action of parasitoids, less so of disease organisms, might be *expected* to depend largely on the density of the population upon which they acted, dense populations suffering greater mortality. These were *facultative factors* maintaining 'a natural balance' of moth populations over long periods (Fig. 11.5). But predation by vertebrates, in contrast to parasitism by insects, might respond *inversely* with insect density, as the numbers of such predators varied less and more slowly than those of their insect prey. So, when the latter were high only a small proportion of them could be eaten, causing the inverse effect. Competition, even for food, operated rarely. These ideas are remarkably close to what many workers believe today. Howard and Fiske's (1911) work was an innovative contribution

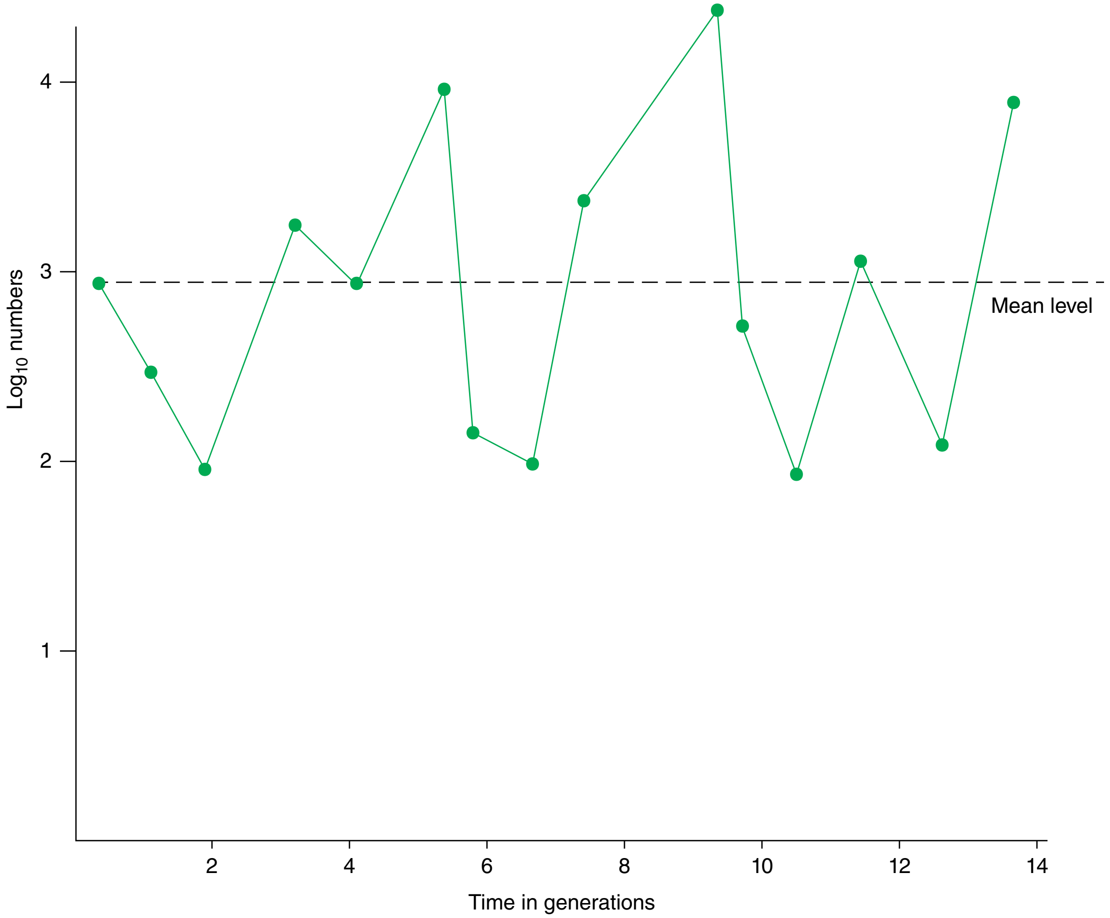


Fig. 11.5. A hypothetical plot of numbers in a habitat on time for a period of many generations. While determined by births, deaths, immigration and emigration the numbers fluctuate irregularly about a mean level.

to population theory. Students should read pages 107–109 of their 1911 paper to appreciate their far-sightedness. One is almost surprised they did not distinguish *top-down* from *bottom-up* effects (Section **10.1**), although they do mention the 'lack' and 'unsuitability' of food, namely its quantity and quality (Section **10.2.2.5**). But to date, because our main focus has been on plant pests, far more is known of their dynamics than of those of disease vectors, carnivores and detritivores, so giving a biased view of insect dynamics.

This brings us to the classical theories of animal numbers. They are important not only for historical reasons, but because *even today* they provide a general framework into which new empirical information and mathematical sub-models can be fitted. Wolda (1995) argues that we should abandon and forget them since they have led to confusion. Murray (1999) notes more sensibly that this confusion is due to a lack of suitable data and scientific rigour. White (2001) calls on 'young ecologists' to make a 'paradigm shift' in the concept of the control of animal numbers. This is unpardonable ageism! Fine. I would only urge them to read the literature first – by which time they will not be so young – to avoid re-inventing the wheel. As a case in point many present workers on metapopulations, but not Ilkka Hanski and Susan Harrison, do not quote Andrewartha and Birch's (1954) early analysis of the subject (their Section 14.2). I believe the classic theories have an essential and enduring place in population ecology, by reason of their comprehensive nature (Hassell, 1998a and b; Hanski, 1998a; Murray, 1999). Science is a matter of building. We may as well forget the Darwins in the development of evolutionary theory. If a theory has not been useful in developing our understanding of dynamics, certainly it can be relegated but never forgotten (Section **11.2.4**). Furthermore, science is not democracy: majorities may be wrong! But it is up to the minority to show them this! While no theory fits all cases (Lawton, 1992), all have a useful place. There is indeed a plurality of dynamical systems affecting insect populations, which we will soon discuss. Even in Lepidoptera, whose populations are the best studied of all insects, a wide variety of dynamical factors affects different species (Dempster, 1983).

Most classical theories, but particularly Thompson's, emphasize that populations must be viewed as global systems. With their unrivalled mobility (Section **10.2.4.1**), a spatial component to insect populations is essential (Freeman, 1976). In the middle years of insect population theory, this fundamental perspective was often lost sight of, for two probable reasons: (i) most deductive models lacked a spatial component; and (ii) most empirical studies took place in patches or small habitats, as Hanski *et al*. (1996) put it, in 'local populations in isolation'. Apart from extensive research by Morris (1963) on *Choristoneura* in New Brunswick and my own field work from 1964–1993, a more general appreciation of the spatial aspects of insect population structure did not arise until the 1990s with the development of empirical metapopulation dynamics, which Thompson, Nicholson and Andrewartha and Birch had promoted long ago.

11.2 Classical Theories of the Control of Animal Numbers

11.2.1 General introduction

Here the term 'control' means, without specifying mechanisms, that insect populations (Sections **9.5** and **9.6**) remain within limits and rarely go extinct (Milne, 1957a). Below is a chronological account of insect population theories with ancillary ideas for other groups. There are two sections. First, several *extrinsic theories* emphasize physical and biotic factors *external* to the focal species, but *tend* to assume that individuals are identical and do not change materially in successive generations. Second, and more realistically, *intrinsic theories* examine the role of individual differences within a population and their environmental and genetic modifications through time. While gene flow and random genetic drift (RGD) have effects (Mayr, 1963; Slatkin, 1985; Petit and Excoffier, 2009), external factors cause direct numerical fluctuations and their huge selective power (Ford and Ford, 1930; Kettlewell, 1973; Kingsolver *et al*., 2001) induce dramatic changes to individuals. Dynamics proceeds on shifting genetic ground (Thompson, 1998), being linked to natural selection. Both theoretical groups have empirical support; indeed they are complimentary. They are related (Section **11.4.1**) to more recent ideas of *top-down* and *bottom-up* factors, and to deductive models (Section **11.5**) that while narrower in approach, are rigorous. Classical theories are central to single species ecology although presently rather out of fashion. Fashion, however, has no place in science, and current discussion, for example, on the meaning of 'population regulation', often proceeds in ignorance of them, much to its detriment. Oksanen (1991) complains bitterly of a similar failing in community ecology. These theories provide a fund of ideas upon which future generations may draw, should they wish.

11.2.2 Extrinsic theories

11.2.2.1 W.R. Thompson (1929, 1939, 1956)

Thompson (Fig. 11.6) is the forgotten man of population theory. Turchin (2003) quotes three papers by Nicholson (Section **11.2.2.2**) but ignores Thompson. He none the less deserves continuing credit since, after presenting early equations of parasite/host interactions (Thompson, 1922, 1924), he framed the first general theory of natural control of animal numbers (Krebs, 1972). His broad attitude was surely due to his extensive work on *Ostrinia nubilalis* (Section **4.4.1.1(d)**) in Europe. He defined natural control as the observed fact that populations of no species *increase without limit*, despite their often great potential to do so. This is '*population limitation*' (an axiom; Sections **11.5.1** and **11.2.1**) due to *individuals* of a given species having 'specific intrinsic limitations', a concept from which 'ecological efficiency' arises (Section **9.8**). This limitation results from 'a complex of factors, varying in composition both quantitatively and qualitatively in different geographical areas or even localities' (Thompson, 1929). Here he touches on global dynamics (Section **12.3.4**). Natural populations cannot not be self-regulating, as Nicholson regards them, since 'the only real beings that exist

Fig. 11.6. W.R. Thompson, the 'forgotten man' of insect population dynamics. In 1929 he developed the first general theory of animal numbers and was one of the first workers to employ mathematical models. Source: Wikimedia Commons.

in the real world are individual organisms, and they alone (if we except the animal societies) have the power of self-regulation or adaptation' (Thompson, 1956). He is well aware of individual variation too. The *individual* is the primary focus of natural selection. 'If we desire to find principles on which to base our theories of populations we must look for them, in the first place, in the behaviour of real entities, which means in the behaviour of individual organisms' (Williams, 1966; Section **9.6**). Łomniki (1988), Leather and Awmack (1998) and Turchin (1999) are more recent advocates of this view.

Species exist in *optimal zones*, favourable to their reproductive success (RS), surrounded by *sub-optimal* and *unfavourable* zones. Due to seral changes in plant communities (a bottom-up effect, Section **2.2.3.1**), to depletion of resources, to pollution by the population (for Nicholson this is competition) and enemy build-up, *these zones change in space and time* (shown brilliantly by Taylor, 1986). Thompson also considers habitat diversity, population fragmentation (metapopulations) and the role of chance: 'the possibilities of existence [of individuals] are quite restricted by the specificity of their requirements and by the great diversity and fragmentation of their habitats, both in space and time'. They must 'move through a network of random events'. (Thompson, 1956, p. 399). While individuals try to track optimal conditions, many fail. When a population is numerous it spreads in *space* and in *time* (Section **2.1**), so reducing population density (the number/density anomaly; Section **9.3**) but meeting sub-optimal or harsh conditions (see Fig. 3 in Stern *et al*., 1959). Recall that natural selection always plays 'catch-up' (Section **9.6**). It relates to what *has* happened (Fisher, 1930; Price, 1972; Wright, 1982a). Individuals can adapt to the future in a heterogeneous environment only by spreading risk (den Boer, 1968, 1998).

Thompson's theory implies the operation of density-dependent movement in space (Grinnell, 1922; Richards, 1961; Lidicker, 1962), and in time (Andrewartha and Birch, 1954) and is *entirely comprehensive* if rather philosophical. 'The fact that there are species, that is, a variety of essentially limited things, means that their ability to increase is necessarily limited.' This is a time-independent statement of objective fact lacking a time-dependent mechanism. While he does not develop the concept of density dependence (Milne, 1957a), he recognizes that *the structure of environmental space* is basic to population (see Berryman, 2002; Section **12.2**), conceives spatial and metapopulation dynamics, and regards the individual as the unit of focus. He distinguishes localized areas of space where a species' RS is positive and others, usually the majority, where it is negative. The latter contains *sink populations,* a principle suggested by Haldane (1956), shown in field data (Freeman, 1981a) and discussed theoretically (Pulliam, 1988; Watkinson and Sutherland, 1995) without proper reference to what had gone on before. So, population sinks (r_m is negative) and population sources (r_m is positive) have spatio-temporal distribution. Sinks are averaged over time (Dias, 1996; Section **11.4.3**), as is r_m here, and so retrospective data are good at detecting them.

Bodenheimer (1928) and Uvarov (1931) wrote in detail on how climate affects population growth. Earlier work on physical factors in insect distribution, survival and reproduction, linking their ecology and physiology (Section **10.1**), influenced them. But they were concerned with *outbreaks*, with the enormous toll that inimical physical factors took on populations and by the fact that insects living in harsh conditions were usually low in numbers. Their work started the 'climatic school' of population ecology, in contrast to the 'biotic school' (Section **11.2.1**), an approach presently resurging (Dempster and McLean, 1998; Turchin, 1999; Walter, 2003). Chapman (1928, 1931), using the analogy of an electrical current flowing through a conductor, compared *biotic potential* of a species to *resistance of the environment*. The former is made up of the species' achieved fecundity (AF), its generation length and its sex ratio. Waage (1982) points out that the last attribute is under-studied in population dynamics. It is, however, an integral part of cyclic budgets (Section **11.4.3**).

11.2.2.2 A.J. Nicholson (1933, 1954, 1958, 1959), A.J. Nicholson and V.A. Bailey (1935)

While not giving it extended mathematical treatment, Nicholson flirted with the deductive approach (Section **11.5**) to populations. Even so, his work following Thompson (1922, 1924), Lotka (1925) and Volterra (1926) is a basis for developing models. Populations are real entities, greater than the sum of their parts, and since they fluctuate within numerical limits they (i.e. *populations*) have innate control mechanisms. These operate *throughout* the density range and arise from aspects of competition, *broadly defined* (Section **9.8**), except at 'a very low level' (see Section **11.2.2.4**). They are assumed *a priori* as necessary to keep balance (Section **11.5.1**). Through time, numbers are 'attracted' to a *median, equilibrium value* or '*steady density*' (see Fig. 11.5), so having a probability distribution around it. They are 'in balance' and 'self-governing' (= Nicholsonian control). But at the edge of distribution, local isolates may not show it (Nicholson, 1958).

Nicholsonian control (= regulation) *is not population limitation* (Dempster, 1983), who says with his usual clarity: 'Regulation is the density-dependent response of the population to an equilibrium level, not merely the depression of the population to levels below the carrying capacity of the habitat'. The latter process is an axiom (Section **11.2.2.1**), the former is a postulate (Section **11.5.1**). It implies that negative feedback constantly *regulates* populations as a result of density-dependent mortality, reproduction or dispersal, and relates to core processes in recent models. The mechanism of regulation is often intraspecific resource competition, which is very Darwinian (above; Section **9.8**). But this is assisted by competition among enemies for whom the focal species is a limiting resource. Thus, *regulation proceeds nearly all the time*, it is *all-pervasive,* the carrying capacity being rarely approached (Milne, 1962; Dempster, 1983). While marginal isolates may not show regulation, Nicholson's point is, I think, that the bulk of a global population is contained in central, often high-density, *core populations* (Brown, J.H., *et al.*, 1995; Gaston, 2009b), which present the big picture (Section **12.3.4.4**). Processes at the margin are usually trivial to global dynamics. But migration, *as a result of competition*, can regulate densities by forcing them into physically harsh areas (Nicholson, 1933), although it is not of necessity evoked by competition of any sort (Johnson, 1969; Taylor, 1986). Note again that even in these early days, Nicholson, as well as Thompson, recognized spatial effects clearly.

While physical factors can limit distribution and *disturb* levels of density by altering habitat favourability, and hence RS, they have no *regulatory* capacity. They are *legislative* (non-reactive) *factors determining the level at which balance occurs*. Weather can destroy, not control. Contra to the climatic school, Nicholson explains that even if bad weather were to kill all but a few of a population, since its effect is capricious and unrelated to density, it could not *regulate* it. Numerical change is not regulation. Competition must do this as its severity relates *unfailingly* to population density. Lacking regulation, numbers would drift away from any level to extinction or to plague levels; a point made more recently (Strong, 1986; Hassell *et al.*, 1989). Contrast regulation with the fate of genes under *RGD*, a classical *uncontrolled* process in population genetics (Fisher, 1922; Lande, 1976; Section **11.2.3.1**). But only a little density dependence is needed to keep undivided populations within limits (Reddingius, 1971, in Strong, 1986; Hanski, 1990). Nicholson (1958) argues that regulation '… permits a species to persist indefinitely in all favourable places' (this is clearly wrong, see Section **12.2.1**). They are well adapted to cope with *fragmentation and variability* of habitats. Indeed, Nicholson and Bailey (1935) describe the essence of metapopulations as: 'small widely separated groups which wax and wane and then disappear, to be replaced by new groups in previously unoccupied situations'. This is very Thompsonian and fits data from suction trapping in the Rothamsted Insect Survey (Taylor, 1986). 'Persist indefinitely' is incongruent with the metapopulation concept, 'wax and wane' is not. Nicholson and Bailey had it right earlier.

Speight *et al.* (1999) illustrate Nicholsonian control using data from Varley *et al.*'s (1973) winter moths. While physical factors cause 89% of juvenile deaths, if we remove the effect of biotic factors that cause the remaining 11% and have a regulatory potential, we can calculate the expected increase in numbers. The sex ratio is 1:1 and AF is 150, under which the per-capita rate of increase λ (Section **11.5**) is ~8. Then the expected number (N_t) after 35 generations (= 35 years) using an initial population (N_0) of 20 moths would be:

$$N_t = \lambda N_0 \text{ which is } 8^{35} \times 20 = 8.11 \times 10^{32} \text{ moths}$$

a number so great that, at 40 mg a moth, they would weigh 5000 times the mass of the Earth! The argument seems compelling, but see below. Most importantly, Nicholson himself (1958) points out the fine edge on which populations are poised. '… if a species which can multiply at the rate of 100 times per generation when unrestricted is subjected to a 99.5% destruction, its numbers will be halved; whereas, if the destruction is 98%, the numbers will double in each successive generation.'

Nicholson's theory requires, following Howard and Fiske (1911), that density-dependent processes *necessarily* balance population numbers, and include competition for resources, cannibalism, enemy action and density-dependent emigration. While physical factors influence the *level* at which balance is achieved (Holdaway, 1932; Section **12.3.4.2**), they cannot provide balance directly. Thus, 'Physical factors may indirectly influence the densities of animals by modifying the positions at which other factors produce balance…' (Point C69, Nicholson, 1933, 1958). Namely, a causal chain. But in this deductive approach there is no need for verification by recourse to empirical data (Royama, 1977), which explains Nicholson's intransigence towards critics. As Russell (1961, p. 54) puts it: 'If the world of sense does not fit mathematics, so much the worse for the world of sense.' He was working within a deductive paradigm (White, 2001).

H.S. Smith (1935) reviewed Nicholson's theory, coining the catchy terms *density-dependent* and *density-independent* factors and emphasizing that only the former could control numbers. Essentially, Nicholson and Smith developed the ideas of Howard and Fiske, making all facets of density dependence and competition, *broadly defined* (Section **9.8**), the central issues in explaining the control of animal numbers. How critical this might be could not be appreciated until more modern deductive analyses appeared (Section **11.5**).

11.2.2.3 H.G. Andrewartha and L.C. Birch (1954, 1984), Andrewartha (1970)

Following Elton (1949), these authors (see Fig. 9.1) warn of the danger of incorporating results of deductive models into analyses of real populations (see Milne, 1957a). Their questions about variation of population density of a focal species in space and time (Section **9.2**), are given in Fig. 11.7. It compares the fluctuation in numbers of three populations of *Austroicetes* (Section **5.2.1.1**(e)), the first

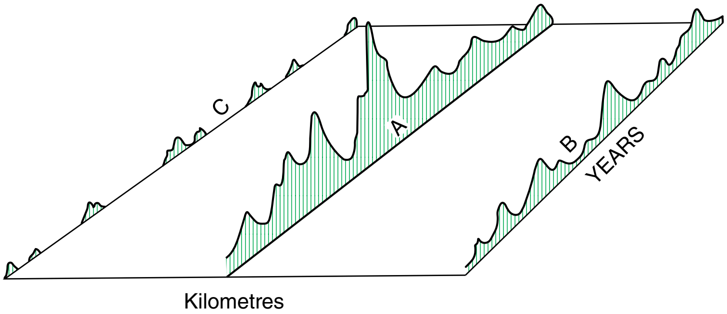


Fig. 11.7. Fluctuation of the numbers of the plague grasshopper, *Austroicetes cruciata*, in three geographical zones. Its numbers are limited either by aridity towards central Australia or by excessive wetness near the coast. Adapted from Andrewartha and Birch (1954) *The Distribution and Abundance of Animals*. Chicago University Press, Fig. 1.2. Reproduced with permission.

in a favourable area, the second in a less favourable one and the third in an unfavourable one. While their figure is hypothetical, it is based on a wealth of field experience of this pest, and so semi-empirical. Its duration is of several years and generations. The longest empirical data sets are from Schwerdtfeger (1935, 1941; Section **11.3.1**; Fig. 11.8) and Tenow (Myers, 1988) jointly recording the numbers of five forest moths.

They use this spatial relationship (1954) to compare dynamics in a '*kind*' region, with those in a '*harsh*' one (Fig. 11.9). The concept is akin to Thompson's optimal and sub-optimal zones and embraces the idea that *weather determines mean population density*, gleaned from the climatic school and as stated in Nicholson's point 69 (Section **11.2.2.2**). Clark *et al.* (1967) note that population processes may well be different in these two zones, and Enright (1976, Fig. 8) models such a difference. In harsh zones the potential for population increase is limited by: (i) shortness of time when the environment is favourable; (ii) reduced RS resulting in (iii) low numbers at the start of the favourable period (A and B in Fig. 11.9). Point (iii) is shown in the moorland moth *Coleophora* (Section **12.3.4.3**) and by the effect of low mean winter temperature on *Myzus persicae* in Scotland (Walters, 1987, in Leather *et al.*, 1993). When such temperature is 2°C almost all die, but at 4°C survival is ~20%, permitting a larger initial population in spring. Also, (iv) there is difficulty in finding resources (Nicholson, 1933). Due to limited individual searching power and some resources remaining unavailable. They regard both physical factors and enemies as having a potential

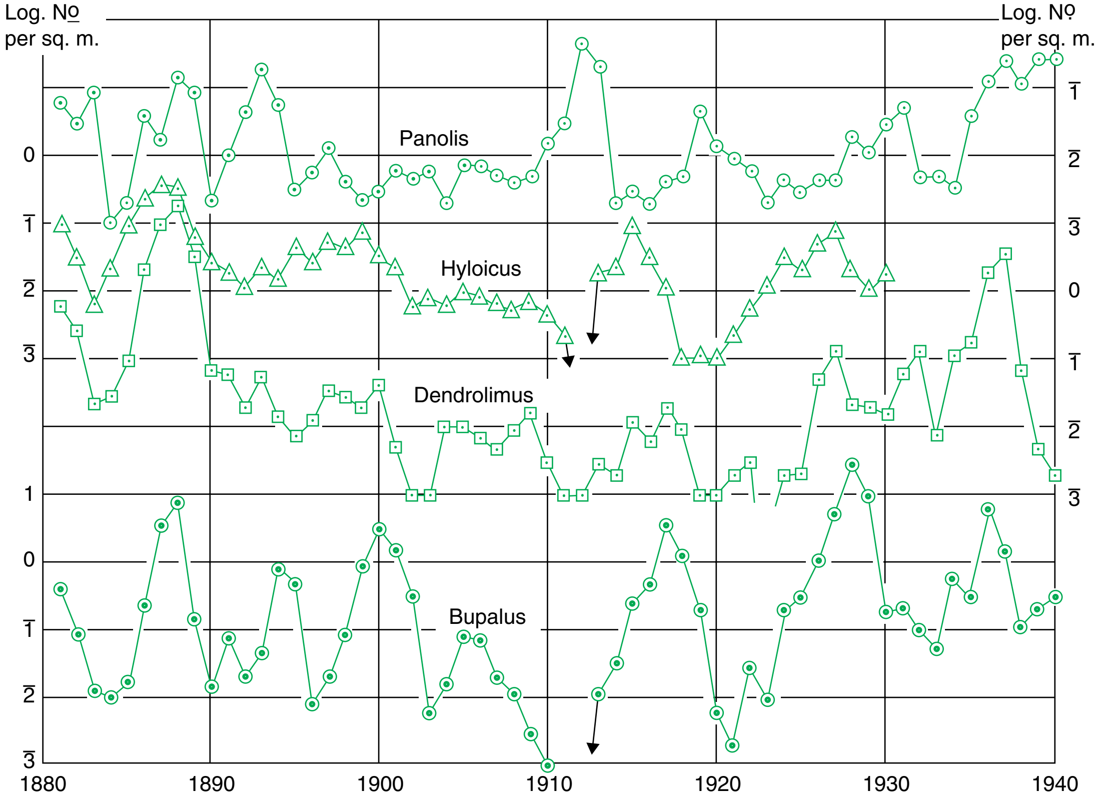


Fig. 11.8. Schwerdtfeger's data on forest moths. The winter numbers of four, univoltine forest moths from a pine forest at Letzlingen, west of Berlin. They represent time-series data in samples from 1880 to 1940. They comprise density estimates for *Dendrolimus* (Lymantriidae) larvae, and *Hyloicus* (Sphingidae), *Panolis* (Noctuidae) and *Bupalus* (Geometridae) pupae. From: Varley, G.C. (1949) Population changes in German forest pests. *Journal of Animal Ecology* 18, 117–122. Cf Fig. 11.5. Reproduced with permission.

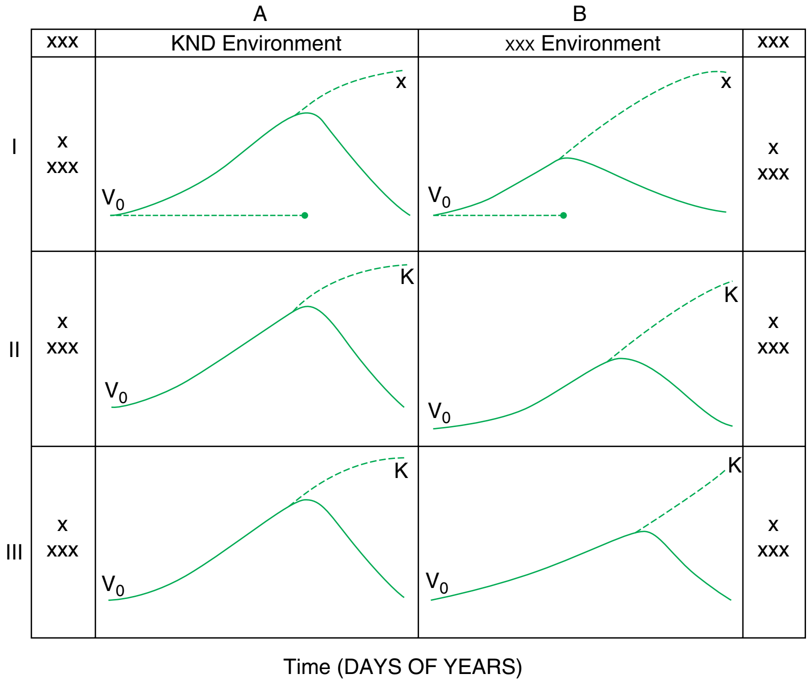


Fig. 11.9. The several effects of harsh and kind environments on the dynamics of a theoretical insect population. After Andrewartha and Birch (1954) *The Distribution and Abundance of Animals*. Chicago University Press, Fig. 14.5, p. 656. Reproduced with permission.

for density-dependent action, an idea from Smith (1935). Limitation of numbers results from the spatio-temporal arrangement and interplay of all such factors, which vary within the area occupied by the focal species.

Emphasizing Thompson's concept that animals live in a spatial framework, populations comprise several local populations interconnected by the movement of their members. Perhaps everyone had read Spencer's (1864) '*Principles of Biology*', who notes '... besides the habitat in which an organism is found there are commonly other habitats, as well or better for it, from which it is absent' (p. 327). Andrewartha and Birch (1954, Section 14.2) give contrasted graphical models of this process, an analysis basic to metapopulation dynamics: an old theme with a new rhythm. They note that the number of individuals comprising a species in a landscape is a function of the *number of local populations* that area contains. This was understood by Nicholson (1933, p. 145) who says: 'Other things being equal, then, the density of a species within the whole countryside varies directly with the fraction of the countryside that provides suitable conditions for the species.' For countryside, read landscape. It is the same principle as, but on a different spatial scale from, the example of aphids on cabbages spaced at different densities in a plot (Section **9.3**).

These authors do not recognize the need for global control of the number of individuals comprising a species. Harsh climates are effective boundaries to mobile populations, weather determining the extent of favourable space in the landscape. As Darwin (1859, Chap. 3) puts it 'the struggle is with the elements in physically harsh environments', while Haldane (1956) remarks 'In these marginal areas selection is mainly against density-independent factors such as frost ...'. But they discuss in detail spatial effects between local populations and are sceptical of the influence of competition, preferring the concept of population limitation (Section **10.2.2.1**) to that of Nicholsonian control. As in Thompson, limitation is subsumed in the idea that harsh peripheral conditions restrict numbers globally. But in empirical data we may find it hard to decide if population limitation or Nicholsonian control is operating. While sophisticated analyses of time-series data are now available (Schaffer, 1985;

Berryman and Turchin, 2001; Turchin, 2003; Brook and Bradshaw, 2006; Sections **11.4.4.2** and **11.5.2**), successive life tables (Section **11.4**) are still a preferable basis for judgement (Dempster and Pollard, 1986; Royama, 1992; Williams and Liebhold, 1997; Murray, 1999).

11.2.2.4 A. Milne (1957a and b, 1961, 1962)

Milne says his theory is a synthesis of pre-existing ones. His term 'natural control', like Thompson's, means *population limitation*: the axiom that populations exist between finite values. He recognizes the distinction between biotic and physical mortality factors, regarding the latter as having no capacity for density dependence as no feedback from the population can occur. Indeed, they may result in local extinction, an early statement of what is held to occur in metapopulations (Harrison, 1991). But effects of enemies depend on factors additional to feedback from their victims. Bad weather can prevent parasitoids searching but only slows host development. Their density-dependent action will at best be statistical (= *imperfectly density-dependent*), or '*density vague*' (Strong, 1986) and may not operate at all. Contrast this with the predictable and perfect density-dependent intraspecific resource competition, which we singled out in Sections **9.1** and **10.2.1**. These factors correspond, respectively, to second- and first-order processes (Royama, 1992; Berryman and Chen, 1999; Section **11.5.1**). But a delay may exist in the numerical response, a *time lag* to increase in enemy numbers to the increased density of their victims (Nicholson and Bailey, 1935; Solomon, 1949; Holling, 1959a; Section **10.2.3.9**). Milne does not make this point, but it is called *delayed density dependence* (Varley, 1947; Morris, 1959) and feedback may be variable (Berryman, 2003). Enemies and adverse physical factors together restrain populations for long periods; intraspecific competition for resources, while rare (Howard and Fiske, 1911; Cornell and Hawkins, 1995), *ultimately* provides population limitation. Populations are not 'in balance', in Nicholson's sense; as Milne sees it, 'the environment rules'.

Data on *Cardiaspina* (Psyllidae) (Clark, 1964) supports Milne's synthesis and explains why biocontrol may or may not be successful. In the lowest zone of Fig. 11.10, the population is in the grip of *Allee dynamics* (Section **10.2.2.4**). Nicholson regards Milne's imperfect density dependence as the density-dependent action by enemies, who *compete* for victims. Milne does not consider cannibalism and says (1957, p. 209) 'there is only one [perfectly density-dependent factor] in Nature for any species ... its own intraspecific competition'. But cannibalism can arise from competition, often as a result of prey shortage (Fox, 1975; Polis, 1981; Section **10.1.2**). Milne (personal communication, 1983) suggests that density-dependent mortality should be tested empirically. Rather than saying a given factor *should* operate in this way from a deductive rationale, one should plot percentage mortality on population density and test the correlation coefficient for significance. Lag effects, heterogeneity of environmental space and redistribution are the main omissions in his theory.

11.2.2.5 T.R.E. Southwood and H.N. Comins (1976), Southwood (1977, 1988)

For brevity we consider these inputs in sequence, although the first is a theoretical population landscape, the other is general descriptions of empirical data. At this point the contrasted evolutionary strategies of *r*- and *K*-selection (Section **9.1**) and their connecting continuum were fitted into a modern population theory. Den Boer's (1968) concept of risk spreading and individual variation also remained to be added.

In the first paper a bounded, theoretical population is analysed with respect to density and the *r–K* continuum. The model is one of *top-down* influence (Section **10.1**). Again, the effect of climatic variation is played down, being regarded as noise and as a component of risk. For species intermediate on the continuum the emergence in the landscape of the *natural enemy ravine* is notable (**Fig. 11.11**). It results from the focal species being partly restrained by, but then outbreeding, its enemies, a situation resulting in the *inverse density dependence* that is often observed (Pimentel, 1961; Stiling, 1987; Hails and Crawley, 1992). This may occur, for example, in psyllid, delphacid and aphidid bugs. Then, *q* and *f*, parameters reflecting the degree of dis-operation (mainly competition) and co-operation in the population. The negative and positive effects of density are also incorporated (see Berryman, 2003). This essentially predictive landscape is compared to some adequate empirical data, work on *Cardiaspina* (Clark, 1964) again being supportive.

In the second input, Southwood uses an empirical approach but retains the effects of *r*- and *K*-strategy

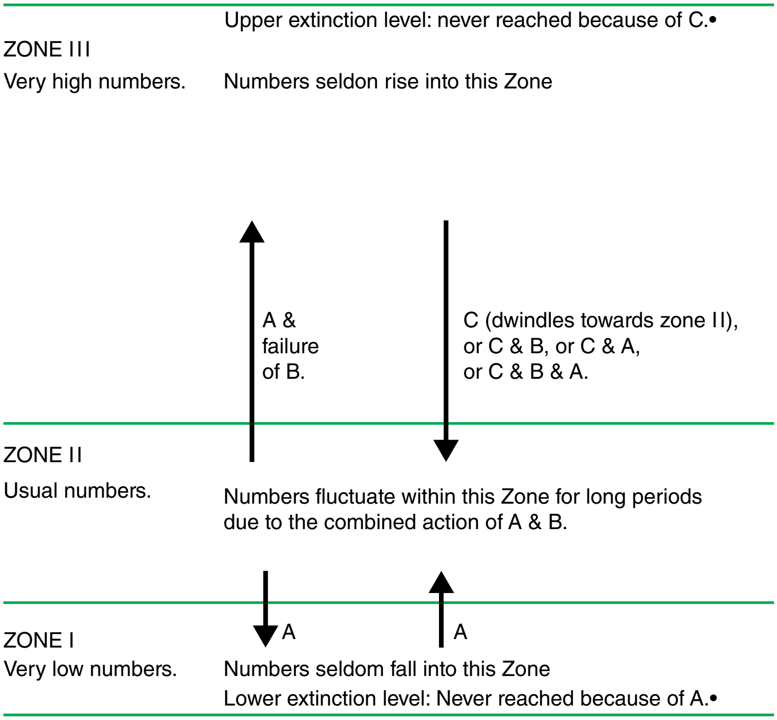


Fig. 11.10. Milne's scheme of population regulation. While populations are ostensibly out of control at low densities their generally high potential rate of increase and the effects of risk spreading (den Boer, 1968) often prevent extinction. Adapted from Milne, A. (1957a) The natural control of insect populations. *The Canadian Entomologist* 89, 193–213. Fig. 2, p. 211. Reproduced with permission.

in relation to real habitat characteristics. The 'habitats' he considers are more like the 'patches' we use in Sections **9.3** and **12.2.1**. The effects of time and space on risk and RS are explored with simple 2×2 matrices. Habitat duration, relative to that of the focal species' life cycle, and its size and spacing provide the '*templet*' against which migratory, survival and reproductive strategies are selected. All of them carry a risk, of course, but it is usually greater for *r*-species. Thus, Southwood explores the ecological basis of evolutionary, indeed of life-history strategy (LHS). He also considers adverse physical factors by including ideas from Grime (1974, 1977), ones related to Andrewartha and Birch's (1954) harsh and kind situations (see Fig. 11.9), later explored by Greenslade (1983). The strength of the model lies in its simplicity, its generality and its links to evolutionary theory. Thus, the nature and spatio-temporal distribution of habitats are the main drivers of an animal's population dynamics and LHS.

While all these extrinsic theories give us some general ideas as to why population numbers stay within limits, *they do not address directly the issue of why most species are rare* (Section **9.4** and Fig. 9.3), although *K*-species are expected to form sparser and more stable populations than *r*-species. Nor is individual variation often examined. In addition, the role of bottom-up effects (Section **10.1**), although a part of Thompson's concept of the suboptimal environment, is undeveloped.

11.2.3 Intrinsic theories 1: Basic effects of individual variation

Unlike extrinsic theories, the ideas examined here are not linked so clearly to specific authors, so we deal with them more generally. Variation in *individual quality*, recognized by Maupertuis in the eighteenth century, and arising from *genetic* and/or *environmental* sources, is now given more weight as it causes strong dynamical effects (Clark *et al.*, 1967; Łomniki, 1980; Rossiter, 1996; Benton *et al.*, 2006; Bonduriansky and Day, 2009; Section **9.6**). Population dynamics meets population genetics

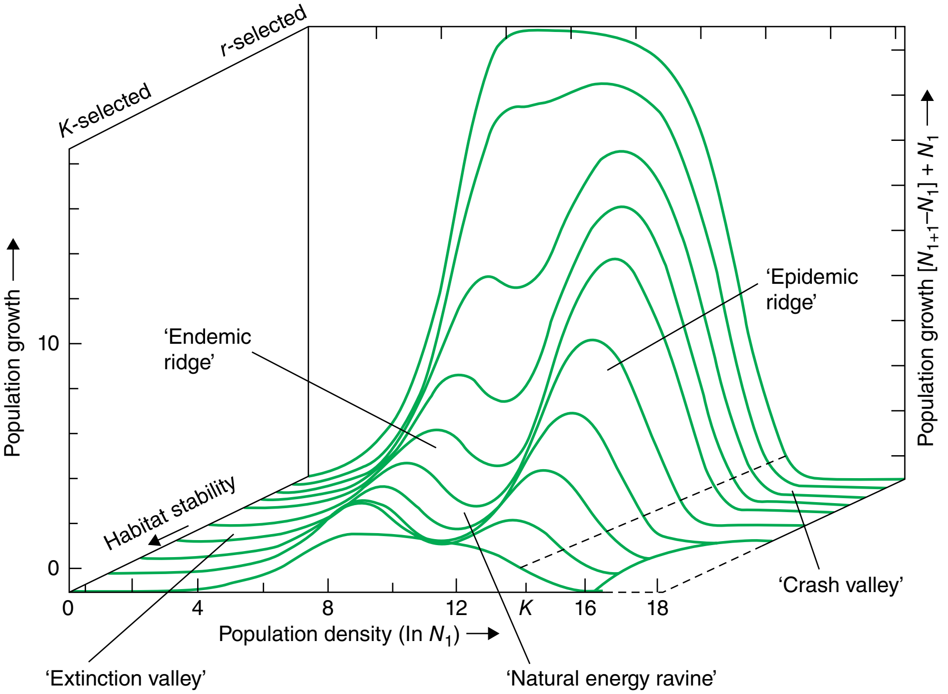


Fig. 11.11. The three-dimensional landscape relates population growth to population density for the continuum of *r*- to *K*-strategists in a closed population. For both extreme *r*- and extreme *K*-species there is a central population density that gives the highest rate of population growth, so that the Allee effect and the deleterious results of high population density are incorporated. Naturally, population growth can be far greater under *r*-selection. Less rapid population change characterizes the *K*-group, who put less into reproduction and more into defence. From: Southwood and Comins (1976) A synoptic population model. *Journal of Animal Ecology* 45, 949–965. Reproduced with permission.

(Section **9.1**). In developing a general empirical theory of insect population (Section **12.3.4**), we will refer repeatedly to genetics. Of course, it is not that external factors are unimportant, but that they operate on variable and changing individuals. Species are not Linnaean (Section **9.10**), they evolve.

While genetic aspects centre on variation in individual quality there are broader features. In a group of related and so *genetically similar species*, some use a variety of resources and have extensive distributions, others are rare and localized (Blows and Hoffmann, 2005). In the UK, three *Tipula* species show this. *Tipula paludosa* is a univoltine, widespread pest of often plague proportions, *T. oleracea* is bivoltine, common, but not abundant and *T. subcunctus* is univoltine, uncommon with a scattered, localized distribution (Freeman, 1964, 1968; Freeman see **12.3.4.1** for more examples). Jermy's (1984) (Section **2.4**) view of the irregular links between herbivorous insects and their food plants is pertinent here and argues for intrinsic components to *commonness and rarity* that reside in but a few genomic differences, albeit polygenic ones (Coyne, 1985; Lande and Shannon, 1996). Recently, the genetic limits to evolutionary change have come into focus (Blows and Hoffmann, 2005; Bridle *et al*., 2009) and often invoked in explaining *range limits*, which of course represent Andrewartha and Birch's first question on insect dynamics (Sections **9.2, 11.2.2.3** and **12.3.4.2**).

Genetic influences naturally affect individual attributes. In *Choristoneura,* variations in AF and egg size correlate with several forms of the maternal X-chromosome (Campbell, 1962, in Ginzburg and Taneyhill, 1994). Then, during development, genetic defects and genomic conflict (Burt and Trivers, 2006) may be lethal. Such intrinsic mortality is distinct from that due to external factors. In the haplodiploid Hymenoptera (and also Thysanoptera and Aleurodidae), a taxon with huge numbers of parasitoids

(Section **8.2.2.5(j)**) and many predators, species are very prone to lose genetic variability in isolates (Graur, 1985; Anton *et al.*, 2007). But past bottleneck effects (Section **11.2.3.1**) may have reduced variability in extant populations (Habel and Schmitt, 2009). In heterogeneous environments individuals would survive poorly. But large populations will slowly generate the genetic variance needed for survival (Fisher, 1922; Lande and Shannon, 1996) because of a mosaic of selective pressures (Section **9.1**). With lycaenid butterflies, Habel and Schmitt point out that genetic diversity is maintained by a high level of dispersal as well as by stable high density. (N.B.: when genetic variation is sought by electrophoresis, one must carefully avoid confounding parasitized or diseased individuals with those having true genetic variability (Wool *et al.*, 1978).)

In *Tribolium castaneum* (Section **6.3.1.2(m)**) there are genetically based dispersive and non-dispersive forms that differ in AF (Ben-Shlomo *et al.*, 1991; Section **11.2.3.1**). The *Pgi* locus determines power output of the flight motor in *Colias* (Watt, 1992) and *Melitaea* butterflies, and thus egg distribution and AF (Haag *et al.*, 2005; Section **10.2.4.1**). Body size and fecundity are usually affected by several genes or loci (Roff and Emerson, 2006), while the genetics of fecundity often involve fitness trade-offs with other life-history traits (Lande, 1982; Section **9.1**; but see Chapuis *et al.*, 2010). Then inheritance may involve *parental (or genomic) imprinting*, where genic expression in the offspring varies according to the sex of the parent donating genes (Chapter 9 in Trivers, 2002). Such effects relate to genetic methods that aim to reduce pest populations (Section **13.2.2**).

But *inherited environmental effects* from non-genetic, largely maternal sources (Kirkpatrick and Lande, 1989; Rossiter, 1991, 1996) also affect offspring quality. They include the amount of yolk donated, which may involve trade-offs between size and number of eggs (Smith and Fretwell, 1974), and food provisioned externally, as in dung beetles and aculeate Hymenoptera. But they also include nuptial gifts from males (Gwynne, 1984, 2008; Boggs, 1995; Section **10.2.5.1**). Other forms of parental influence are the orthopteroid ootheca, solitary wasp cells and, more generally, egg distribution (Section **10.2.5.2**). Secondary plant compounds (Section **2.4.2**) can be sequestered by either parent and passed to offspring, who use them in defence. So, the physico-chemical factors experienced by a parent may influence intrinsic qualities in the offspring (Anderson, 1968). Indeed, the *parental environment* (Rossiter, 1996) has complex effects on the progeny, naturally the closest link being between mother and embryo (Mousseau and Dingle, 1991).

Apart from genetic variation in the focal species, variation is generated in a bottom-up direction from food plants, prey and hosts. In the field, there were strong effects of both plant genotype and external drivers on numbers of *Asphondylia borrichiae*, the gall midge of *Borrichia* (Stiling and Rossi, 1996), while Yukawa *et al.* (2016) record strong bottom-up effects on the dynamics of *A. sphaera* galling *Ligustrum* fruits. In *A. borrichiae* there were interactions between plant genotype and other external factors, a result that would leave those who labour to develop resistant crops unsurprised (Section **13.2.4.2**). In addition, their work and that of others (Section **10.2.3.8**) shows that plant quality modifies the impact of the top-down pressure from enemies. We are now in a better position to discuss these intrinsic effects on populations in more detail.

11.2.3.1 Intrinsic theories 2: Further effects of individual variation

Intrinsic approaches to dynamics being complex, we need to expand the outline discussed in Section **11.2.3**. Variation, and of course mutation upon which it depends ultimately, is the raw material of natural selection. The powerful selective forces operating on insect populations must induce rapid and significant changes to their genetic structure (Ford, 1931), while Nicholson (1933, p. 139) points out that natural selection 'must continually tend to destroy any such balance [of population] that may already exist'. Animals continue to evolve (Haldane, 1956; Trivers, 1985); they have *evolvability* (Houle, 1992; Jones *et al.*, 2007; Section **9.1**). In insects, selection must be massive since while their populations often fluctuate widely (Varley, 1949; Dempster, 1983; Baltensweiler, 1993), even modestly fecund females each lay ~100 eggs, causing a potentially rapid increase in population (Sections **11.2.2.2** and **11.5.2.1**). As such increases occur rather rarely, being restrained by mortality while juvenile (Cornell and Hawkins, 1995; Hawkins *et al.*, 1997) and failure to reproduce as adults, strong selection is implied (Jones, 1999). Variations in fertility (Fisher, 1930; Morris and Miller, 1954; Taylor, 1975; Heisswolf *et al.*, 2009; Sections **10.2.5** and **11.4.1**) also play a role and depend primarily on *parental quality*, from whatever cause. When populations increase under 'kind' conditions selection is less, permitting many inferior genotypes to survive. But after periods of strong adverse selection resulting in low numbers, only the very fittest remain (Holling, 1959b; Ford, 1975). So, regulation of numbers proceeds on genetically variable populations, fitter after harsh selection, weaker after a benign period, providing an intrinsic element to dynamics.

Ford, like Dobzhansky, is a major figure in the development of ecological genetics. For many years he and his father studied a small isolate of *Melitaea aurinia* (Nymphalidae) as a field example of changing numbers and variation (Ford and Ford, 1930; Ford, 1975). In a period of sustained population increase and relaxed selection, they found many weakly flying butterflies and diverse wing patterns. *Fitness was inversely related to numbers*, albeit with a time lag, giving a negative feedback. Ford (1931), following Fisher (1922), emphasized the principle that in extensive habitats, in contrast to small isolates as in *Melitaea*, a species would adapt to a wider range of conditions, so maintaining greater genetic variability. I suggested (Section **10.2.4.1**) that this occurs in wide-ranging HISC insects. Conversely, there is close adaptation in England of the butterfly *Papilio machaon* to its local fenland habitat (Section **12.3.4.3**). Habitat heterogeneity drives a selective mosaic and so genetic diversity (Wiens, 1976; Nevo, 1983; Sugg *et al*., 1996; Section **12.2.2**). Insects adapt to this heterogeneity by genetic and phenotypic plasticity, the former depending on a fund of variation generated by mutation and sexual reproduction (Birch, 1960; Bürger, 1999). Polymorphisms are a part of this variability and maintained by complex processes (Ford, 1975), especially pleiotropy (Gimelfarb, 1992). But *adaptation is limited by genetic possibilities* (Punnett, 1912; Bradshaw, 1991; Blows and Hoffmann, 2005; Bridle *et al*., 2009; Section **9.1**) and because natural selection always plays catch-up (Sections **9.7** and **11.2.2.1**).

Since some alleles are rare, small populations are deficient in them. Unlike large populations they possess less of the species' *gene pool,* especially in marginal isolates. Fluctuations in their numbers may entail further gene loss, although relatively survivors will be the fittest. This process of *random genetic drift*, in which chance plays the key role (Fisher, 1922; Wright, 1931, 1975), is for statistical reasons strong in small populations, especially so when reduced to very low numbers (Waddington, 1957, personal communication, 1958). These events are now called *bottlenecks* (Nyabuga *et al*., 2010). Variability can be regained only with new mutations, genetically novel immigrants and increasing population size. While gene loss is rapid, re-acquisition may be slow, especially when by mutation alone. A classic case is the appearance in Bogota of a small population of *Drosophila pseudoobscura*, presumably from a plane. The estimated mean number of alleles per locus (a simple measure of variability) was 1.38 compared to 2.67 in the North American population from which it likely originated (Prakash, 1972, in Nei *et al*., 1975). Such low genetic variation in isolates makes them vulnerable to inimical factors. They have fewer genes with which to respond to environmental vagaries and are less likely to generate mutations. Also, mutant pairs may work well together but not alone (Endler and McLellan, 1988). In some species particular genes or gene combinations are advantageous at high densities. For example, in dense groups of *D. pseudoobscura* the chromosomal inversion 'Standard' is favoured over 'Chiracahua' (Birch, 1960). Such gene arrangements decrease by selection at low density. In the polymorphic damselfly *Ischnura elegans* (Section **9.8**), blue females have an advantage at high density over brown ones. But again adaptation plays catch-up.

When genetic differences exist between non-migrants and migrants, as is often the case, emigration leads to a reduction of genotypes and genes coding for migration. Now two alleles, say *A* (dominant) and *a* (recessive), produce three genotypes, *AA*, *Aa* and *aa*. In endopterygotes, *AA* and *Aa* generally code for brachypterous non-migrants (Roff, 1994). If the gene for staying were recessive, such a population would soon be bereft of genes coding for migration. But here the *A* gene *is* so expressed and spreads as brachyptery may be beneficial by conferring higher fecundity (Zera and Denno, 1997) and because *a* genes are lost in emigrants, especially as they engage in so hazardous an activity (Harrison, 1980). Since only *aa* individuals emigrate, some *a* genes stay put in the heterozygotes. Of course, immigrants are exclusively *aa* and may arrive in numbers, augmenting frequency of the *a* gene. Selection against this gene would be great, however, unless heterozygotes had a special advantage in residents (Harrison, 1980). But pleiotropic effects are possible as in Watt's *Colias* butterflies (Section **10.2.4.7** and Watt *et al*., 2003). In exopterygotes brachyptery is generally polygenic, leading to the spatial spread of genes coding for it (Roff, 1994). In several cases, however, winged forms are induced environmentally (Johnson, 1969; Harrison, 1980), either by inadequate food, crowding, or both. Such induced effects occur in aphids (Lees, 1966; Toba *et al*., 1967; Taylor, 1975) and *Melittobia* (Sections **8.2.2.5(p)** and **10.2.4.6**; Schmieder, 1933; Freeman and Ittyeipe, 1982; Matthews *et al*., 2009). Of course, in desert locusts (Section **5.2.1.1(a)**), crowding induces the migratory phase, but all adults can fly.

For the water bug, *Gerris lacustris*, alternative alleles code for wing length, with *aa* long-winged, *Aa* short-winged and *AA* lethal (Poisson, 1924, in Harrison, 1980; see Section **10.2.5.2**). While this work has been questioned, it may be a further case of *genetic make-up causing direct mortality*. As in human sickle cell anaemia (Section **7.3.2.4(d)**), such a mechanism evolves only under heterozygote advantage (= over-dominance), as Fisher (1922) noted. Another possibility is that heterozygotes migrate only when adverse conditions dictate. Thus, both genes and environment could influence dynamics through migration (Roff, 1994), who makes the point that only if migrant females mate with brachypterous males before leaving, could the gene for brachyptery spread to new habitats. The evolution of brachyptery may depend critically on the persistence of the habitat or patch (Harrison, 1980), and so is maladaptive where this is short (Section **12.2.3.2**). New genetic material entering a population with immigrants leads to hybridization, which has diverse consequences. Rarely, hybrids are fitter than either parental stock (Barton, 2001), leading to *introgression* into one or both populations (Mettler *et al*., 1988), so causing a cline. It may be explained through the segregation of additive genetic factors, with epistasis playing a limited role. Several cases exist in which *hybrid species* are formed through the failure of assortative mating (Bullini, 1994).

To go back, Sewall Wright (1932, 1982a) argued reasonably that selection in isolates with minimal immigration would result in gradual genetic adaptation to the locality. He termed the result as an *adaptive peak* in a three-dimensional *genetic landscape*, concluding that this process could lead to speciation. Locally favoured combinations could not be undone by selection in a constant environment, because individuals would be increasingly disadvantaged if they descended into *adaptive valleys*. More realistically favoured genotypic combinations are constantly assailed by a changing environment and so selection, and also by RGD and migration. Namely there exists a *shifting balance* (Wright, 1982b).

His theory has been under close scrutiny fairly recently (Gavrilets, 1997, 1999; Coyne *et al*., 2000) although not for the first time (Fisher, 1941; Moran, 1964). Even so, Wade and Goodnight (1991), using cultures of *Tribolium castaneum*, found support for Wright's theory. Gavrilets explains that a genetic landscape is not simply three-dimensional (Wright 1982a, p. 431–432, is clearly aware of this), and so it may be a misleading metaphor. He proposes a multi-dimensional landscape with connected networks of very fit genotypes separated by 'holes'. Populations could evolve towards reproductive isolation by following a 'ridge' of such genotypes without crossing 'any deep adaptive [maladaptive] valleys' (Gavrilets, 1997). Coyne *et al*. (2000) conclude that Wright's hypothesis 'invokes a specific [and improbable] concatenation of drift, selection and differential migration'. Another model (Gavrilets, 1999) suggests that speciation is facilitated in a metapopulation of small units despite limited gene flow within it. Coope (1979), having studied Cenozoic fossil beetles extensively, concludes that some species have maintained specific identity for at least 1.6 million years. Because of their mobility on so long a time scale, barriers to gene flow were broken down. Speciation did not occur when 'gene pools were … kept well stirred'. When species are confined in a changing environment, adaptive evolution is the alternative to extinction. Coope's beetle species are based on fossil morphology; we recall (Section **9.10**) that morphologically identical sibling species may have quite different biological properties (see Section **12.3.4.4(e)**).

Considering criticisms of Sewall Wright, students note: (i) that for over five decades he made important contributions to the genetics of evolution; and (ii) that hypotheses are essentially iterative. Again we recall that genetic imperatives can engender reduced RS, which has consequences for population dynamics. For reviews see Section **9.10**; Mayr, 1963; Coyne, 1992; Bush, 1994; Gavrilets, 1997, 1999; Coyne *et al*., 2000; Coyne and Orr, 2004; Turelli and Orr, 2000; Turelli *et al*., 2001; Barton, 2001; Schluter, 2001; Bürger *et al*., 2006.

Carry-over effects from generation to generation are not solely genetic because nurture as well as nature is involved (Kirkpatrick and Lande, 1989; Mousseau and Dingle, 1991; Rossiter, 1996). While an individual might be 'fit' genetically, if it had survived harsh conditions during development, it would have reduced reproductive prospects in comparison to a genetically identical individual that has experienced better conditions. Of course, females deprived of adequate food would be smaller and so less fecund than normal (Honěk, 1993), as in butterflies, forest moths, blow flies and solitary wasps (Sections **10.2.2.5** and **10.2.5.1**). Even so, this outcome would be abolished in the next generation if environmental conditions improved.

While the study of *inherited environmental effects* became popular in the 1990s (Rossiter, 1991, 1996), a classical example of intrinsic, carry-over effects came earlier. Wellington (1957, 1960) researched the role of *individual difference* in the dynamics of the forest moth *Malacosoma pluviale* (Section **5.2.1.4(e)**). Larvae in expanding populations built elongated webs and fed actively outside them. But when falling from peak densities they built compact webs, fed less, had higher mortality and produced adults with lower AF and less mobility. A probable reason for high larval mortality is that the eggs contained less yolk. Even so, for *Zeiraphera diniana* (Section **5.2.1.4(d)**), Clark *et al.* (1967) suggested that the 'strong' and 'weak' physiological races, which alternate in their population cycles, would have a genetic basis, which proved to be true (Baltensweiler, 1993). These races vary in their ability to resist parasitoids and granulosis virions. Also, viral and protistan diseases can be transmitted trans-ovarially (Ginzburg and Taneyhill, 1994), also giving carry-over effects. In gypsy moths, viral survival during winter on the eggs affects their dynamics the following year (Dwyer *et al.*, 2000). While female quality takes centre stage, recall that genetic quality of males is embodied in fertile eggs, while mating frequency and paternal investment often enhance fertility (Section **10.2.5.6**). This has been little studied (Zera and Denno, 1997). But in *Z. diniana*, outbreaks are due to *assortative mating* within the dark morph and result in close synchrony with larch bud burst.

Other inputs to intrinsic theory, largely in relation to mammals and birds, came from Chitty and Wynne-Edwards. In voles, Chitty (1960, 1967) found that stress-related changes due to conflict at high densities produced individuals of diminished quality. Reduced RS, population crashes and ultimately cycles resulted. Terrestrial vertebrates are often territorial and according to Wynne-Edwards (1962) may limit their own densities by competition for conventional goals before the existence of resources is at risk. Since such actions could involve group selection (Section **9.6**) his theory has had little following (Trivers, 1985). Its value lies in raising questions and documenting phenomena. Wynne-Edwards says (p. 20): 'Evolution [at the level of the social group] can be ascribed ... to … group selection – still an intraspecific process, and, for everything concerning population dynamics, much more important than selection at the individual level.' Unlike Sewall Wright, he emphasizes differential extinction rather than differential productivity. Group selection, at least in models, is confounded with kin selection and sex ratio theory (Maynard Smith, 1964, 1976; Williams, 1966; Wilson, 1983; Hamilton, 1996), but a deeper examination here is inappropriate.

Pimentel (1968) drew attention to genetic feedback mechanisms as important components of population control. Working with Al-Hafidh on laboratory populations of house flies and the parasitic wasp *Nasonia*, he showed that co-evolution of genetic changes led to less numerical fluctuation. But variation in maternal quality *per se* may drive the cyclical behaviour of some forest moth populations (Ginzburg and Taneyhill, 1994), as Wellington (1964) originally suggested for *Malacosoma* (but see Berryman, 1996).

Genetic and environmentally induced changes are not confined to the focal species, but a property of the biotic environment. Plants can reduce their quality as food for a herbivore leading to its reduced RS, a bottom-up effect (White, T.R.C., 1978). Indeed, we have capitalized on such effects to develop resistant crops. A *status quo* in biotic interaction does not exist. Evolution is omnipresent (Trivers, 1985) and often rapid (Benton *et al.*, 2006). Plants evolve diverse ways to resist herbivory; herbivorous insects evolve like means to circumvent them, leading to a co-evolutionary arms race (Section **8.2.1**). Plants may have had greater impact on insect dynamics than vice versa, although little is known of the latter (Crawley, 1989; Section **8.2.3**). Predators and their prey also evolve, leading to various outcomes (Juliano and Williams, 1985; Abrams, 2000). The rationale of sexuality itself may, at least in part, relate to this race, an adaptation in larger, more slowly breeding animals, to permit them to stay ahead of faster breeding parasites (Hamilton, 1980). Keeling and Rand (1995) believe that the genesis of spatially extended genetic variability could be effective too. Insect vectors of parasites of vertebrates often have very low levels of infection (Sections **7.3.2.4(b)** and **7.3.2.4(m)**). Why is that? Also, the genetic diversity of victims may make it difficult for enemies to overcome them.

The likelihood that a population may not be structured genetically in subsequent generations as it was initially, leads to a dynamic view of temporal density dependence. While appropriate statistical analyses may reveal significant effects (Section **11.4.4.2**), neither victims nor enemies may be the same genetically at the end of the study as they were at the start. Density dependence is not invalid, however, it proceeds on the shifting genetical sands of co-evolution (Section **8.2.1**). Like reasoning applies to spatial density dependence.

11.3 Empirical Time-Series Data

These are sequential estimates of numbers or densities, often called loosely 'abundances', usually at one stage of a species' life cycle. When at a single stage they are not affected by the number/density anomaly (Section **9.3**). Usually there are no estimates of mortality. They have been in vogue over the last 25 years and even alone provide useful facts (Halley and Inchausti, 2002; Turchin, 2003; Brook and Bradshaw, 2006), ones amenable to detailed analysis. One tries to connect numerical patterns with ecological processes. They should span at least 20 generations. Life tables often provide detailed facts over a more limited period, but like time series, gain accuracy the longer the period. Short runs fail to sample variation adequately (Hanski, 1990; Cyr, 1997; Turchin, 2003) and spectral analysis of data is inefficient. Recently, wavelet analysis has been found to be appropriate (Cazelles *et al*., 2008), as it is useful in decomposing non-stationary systems.

Beginning students note that population increase is multiplicative, not additive, and so often displayed in logarithms. Population numbers vary through time under the influence of many factors, genetic and environmental, positive and negative, ultimate and proximate (Section **12.3.2.1**). Many operate concurrently. Thus, we are warned (Royama, 1992; Williams and Liebhold, 1997; Hunter, 1998) that such analyses may be too limited to diagnose these influences (below) and to assess the degree with which they act. For example, are they density dependent (Berryman and Turchin, 2001)? Then Freckleton *et al*. (2006), endorsing Pollard *et al*. (1987), have shown that census errors in small samples may indicate strong density dependence, when in reality it is weak or absent, giving a false impression of population processes. Hunter believes that they are most useful as *an adjunct to life-table data*. To my mind, and for Pollard *et al*., they are no substitute for life tables, and analogous to what statisticians call a '*quick and dirty*' method. Even so, if correlated to components of weather they may contain some non-proximate factors that life tables may not reveal. But in general they would provide better information if the number of eggs and the number of adults entering a generation could be estimated *independently*.

Apart from these caveats and before detailed analyses are made, much information is revealed by plotting $\log_{10}$ numbers on time (Varley *et al*., 1973; Royama, 1984; Myers, 1988; Turchin, 2003). Time is measured best in generations and, as most studies are made in temperate regions, these are often annual. Such simple plots address several questions: (i) Do numbers fluctuate about a mean level? (ii) What is the amplitude of fluctuation? (iii) Does extinction occur? (iv) Applying further analyses, is there evidence for density dependence, (v) cyclic behaviour and (vi) chaos? Relating to Andrewartha and Birch's third question (Section **9.2**) and rarely discussed is, (vii) how is the *level* about which numbers fluctuate determined? (Nicholson, 1933; Freeman, 1976). Thompson's and Nicholson's theories of population would have been on firmer ground had they been related to long time-series data, showing what Nicholson asserted and most workers thought, that populations are controlled. But they could be regulated in a Nicholsonian manner or restrained by population limitation (Murray, 1979; Dempster, 1983). Also note that subsequent theories emerged after several sets of pertinent data had surfaced or had been recorded (Miller and Epstein, 1986).

For points (i) and (ii), Pimm (1984) and Grimm and Wissel (1997) complain that the term 'stability' has often been used loosely (see Holling, 1973; Antonovics and van Tienderen, 1991). It could refer to low numerical fluctuation of a population (*constancy*) and so to lack of change in the mean level about which numbers vary, to a quick return after a perturbation (*resilience*) or simply to *persistence*. Then, apart from populations, stability may be applied to the floras, faunas and ecosystems. Thus, when the term is used (as with *competition* and *abundance*), the aspect it refers to must be specified. McArdle and Gaston (1995) discuss ways of estimating general temporal variation. In insects the amplitude of population fluctuation is variable, from an order of magnitude for some Dutch carabid beetles (den Boer, 1998) to five orders for a Swiss population of *Zeiraphera* (Section **5.2.1.4(d)**;

Baltensweiler, 1993; Turchin, 2003). To estimate such fluctuations, note that we need long runs; short runs are inadequate (above; Lawton, 1988): variation is a function of time. In particular, the long-term effects of physical drivers will be missed. For point (iii), it is impossible to know if a field population is extinct or merely too low to be revealed by the intensity of sampling (Taylor, 1990; McArdle and Gaston, 1995), as this usually amounts to only a few per cent of the area occupied. For point (iv), density dependence in time-series data has been sought traditionally by auto-regressing the current population density, N_t, to past densities, N_{t-1}, N_{t-2}, … N_{t-d}, and applying an exogenous input of 'random shocks' (Royama, 1977, 1992; Berryman and Turchin, 2001). The latter authors developed a *partial rate correlation function*, designed specifically for ecological systems analysis, which has proven to be superior to others in detecting underlying density dependence.

For point (v), population cycles have long been a big field in animal ecology from the work of Charles Elton and Patrick Moran who in the 1940s and 1950s investigated fluctuations in Canadian lynx numbers. Oddly, they occur in insects and mammals but not in birds (Pimm and Redfearn, 1988). Why is that? Randomly generated time series, however, always contain a cyclical component and if smoothing is attempted, for example by taking a two-point moving average, this will generate further cyclicity (Cole, 1958). Maynard Smith (1989) notes that it is 'fatally easy to read pattern into stochastically generated data'. But ostensibly, real cases of cyclicity occur from the confines of jars of experimental beetles to spatial scales >1000 km (Utida, 1957; Auslander *et al.*, 1974; Berryman, 1996; Ranta *et al.*, 1997a and b; Hassell, 1998b; Berryman and Chen, 1999; Section **11.5.2.3**). Furthermore, pattern may well be dependent on scale (Wiens, 1989; Brook and Bradshaw, 2006), and Holling (1992) makes a case for the existence of cycles of different periods (3–5, 10–15, 35–40 and >80 years) in the dynamics of caterpillars defoliating North American boreal forests.

Insect population cycles with wide fluctuations should be relatively error free, but occur in the field in a minority of species (Lawton, 1988; Pimm and Redfearn, 1988). Again there are two aspects: (i) cyclicity in a single population; and (ii) correlated cyclicity in two or more annectant, or even distant, populations (Mason, 1978; Miller and Epstein, 1986; Ranta *et al.*, 1997a). For point (i), real cyclicity could result from extrinsic and/or intrinsic drivers. Some workers suspect that weather drives the cycles in *Choristoneura* and winter moths (Sections **5.2.1.4(c)** and **5.2.1.4(g)**). But from early modelling interactions of parasitoids and their hosts (Thompson, 1922; Lotka, 1925; Nicholson and Bailey, 1935), cycling of both interactants was predicted and observed. First-order processes may drive rapid cycles, especially intraspecific competition (Berryman and Chen, 1999). Second-order feedback processes may drive longer cycles (Berryman, 1996; Turchin, 2003; Section **11.5.1**), which could involve effects from food quality, parasitoids or pathogens in the previous generation. Cycling is also affected by the per capita rate of increase r_o, (Ginzburg and Taneyhill, 1994; Section **11.5.2.1**).

Correlated cyclicity in separated populations is known in some British butterflies (Pollard, 1991; Sutcliffe *et al.*, 1996), moths and aphids (Hanski and Woiwod, 1993), nearby population units of carabid beetles (van Dijk and den Boer, 1992) and in mammals (Ranta *et al.*, 1997a and b; Swanson and Johnson, 1999). The effect has value when forecasting outbreaks, which may well occur over wide areas. Liebhold *et al.* (2004) give a review, emphasizing spatial synchrony in natural environments. The traditional explanation of regionally correlated climatic factors as drivers is valid (Berryman, 1996; Kendall *et al.*, 2000). But the *associated effects* of migration are important, especially over relatively short distances (Sutcliffe *et al.*, 1996) and when density dependent (Swanson and Johnson, 1999). These effects must be appreciated when considering spatial models of populations (Section **11.5.3**) and empirical data on global dynamics (Section **12.3.4**).

The search for chaos became popular in the 1990s (Hassell *et al.*, 1991) and remains a significant feature in analysing time-series data. Chaos is a '*sensitive dependence on initial conditions*' (Hastings *et al.*, 1993; Turchin, 2003), meaning slight differences in parameter values in the equations lead to very different end results. Although to non-mathematicians it means *a state of disorder*, chaos is not stochasticity. In the short term, chaotic systems are deterministic and predictable, stochastic systems are unpredictable over any period. The level of chaos in time series may be estimated by the *Lyapunov exponent* (λ), a measure of the rate of divergence of two *nearby* initial conditions (Ellner and Turchin, 1995). Chaotic systems ($\lambda > 0$) amplify the perturbations ('noise') *already present* in the system, non-chaotic systems ($\lambda < 0$) dampen them. Positive values of λ lead to chaos, negative ones to less fluctuation. But since the 'initial conditions' in a population change with time, so do the Lyapunov exponents, populations are more prone to become chaotic at some times than at others. In northern Fennoscandia, vole dynamics show a blend of order and irregularity such as would occur in a noisy chaotic system (Turchin and Ellner, 2000).

11.3.1 The numbers of lepidoptera

The now celebrated density estimates of four, univoltine moths from a German forest were missing from early theorizing (Schwerdtfeger, 1941; Varley, 1949; see Fig. 11.8). They show the following: (i) recalling the great potential for population increase, there is evidence of regulation about a mean; (ii) an amplitude in density change of two to three orders of magnitude (*Zeiraphera*, Section **5.2.1.4(d)**, is even more variable); (iii) evidence of cycling; and (iv) in *Dendrolimus*, *Hyloicus* and *Bupalus* there are, *ostensibly*, single extinction events. 'Ostensibly' since they almost certainly existed at densities too low to be revealed by the sampling intensity (see den Boer, 1985; Section **11.3**). Estimates for the moths are comparable as they are all made in the same instar. *Bupalus* pupae had a mean density over the years of ~100/m^2, while the other two species varied around a mean of ~10/m^2 or, more impressively, ~1,000,000 and ~100,000/ha. Recall, as with tree leaves (Section **10.1**), larvae occupy three-dimensional space but pupae in the soil effectively occupy two-dimensional space. These data had been accruing for ~50 years even when Thompson's and Nicholson's theories were propounded! Not to mention the 100-year study of Scandinavian winter moths (Tenow, 1972, in Myers, 1988; Section **5.2.1.4(g)**). Such omissions in science are found in the marginalization of Maupertuis' studies on inheritance, Patrick Matthew's failure to develop natural selection (Section **11.1.2**) and Mendel's entombed results. What more treasures remain buried?

But further data exist. For *Zeiraphera* in Switzerland, there are records similar to Tenow's for ~70 annual generations (Baltensweiler, 1964; Myers, 1988), which vary about a mean. In good estimates from 1945–1961, these have an amplitude of approximately four orders of magnitude, but there is stronger evidence of cycling, with a period of ~ 8–9 years (see Fig. 9.1 in Turchin, 2003). From Canada, long-term data for *Choristoneura fumiferana* (Section **5.2.1.4(c)**) have been analysed by Morris (1963) and Royama (1984), and for *C. pinus* by Foltz *et al.* (1972). From Denmark, Münster-Swendsen (1991) records data for the tortrix *Epinotia tedella*. There is evidence for 6–8 year cycles, probably driven by sub-lethal infections of *Mattesia* spp., a neogregarine having a delayed effect on AF. For *Bupalus piniarius* (Geometridae) data exist from the Netherlands from 1950 to 1963 (Klomp, 1966), from Scotland from 1954 to 1978 (Barbour, 1985), with work continuing to 1996 (see Fig. 10.33 in Speight *et al.*, 1999). Again, evidence exists of control and cycling. In the north of Scotland *Panolis flammea* has mildly cyclic populations of 6–7 year duration on *Pinus contorta*, their amplitude apparently suppressed by spraying insecticides (Hicks *et al.*, 2001). Varley *et al.*'s (1973) results (Section **5.2.1.4(g)**) for the winter moth run to 16 annual generations, but Roland (1998) gives more data, also with evidence of cycling. Tenow's survey for this moth from Scandinavia (above) gives population peaks at 9.4 years. Hunter (1998) published Varley *et al.*'s results for *Tortrix viridana*, sampled along with the winter moth. Other data are those of Mason (1974, 1976) for *Orgyia pseudotsugata*, and of Gargiullo and Berisford (1983) on the comparative dynamics of two *Rhyacionia* tortrix moths. More time series can be found in Miller and Epstein (1986), Berryman (1988) and Turchin (2003).

In orchards, data exist for the codling moth (MacLellan, 1977) and *Epiphyas postvittana* (Danthanarayana, 1983), both tortrix moths. In fields, Harcourt (1957) worked on diamond-back moth dynamics (Section **5.2.1.4(a)**), while Dempster (1982) studied cinnabar moths. In Japan, Ito and Miyashita (1968) give life tables for another arctiid moth *Hyphantria cunea,* while Watanabe (1981) studied the swallowtail butterfly, *Papilio xuthus*. This list is not exhaustive and apart from Lepidoptera, more studies exist on sawflies (Cornell and Hawkins, 1995). So the Lepidoptera, being major pests of forest, orchard and field crops, are well covered (Hawkins *et al.*, 1997). Dempster (1983) gives an insightful review of their dynamics.

11.3.2 Mainly the numbers of other insects

Research on other major orders is far less extensive. In addition, while Schwerdtfeger's, and Gargiullo and Berisford's data show the value of comparative studies (Section **2.1**; Price, P.W., 1997), they are for different species not *different localities*. What is still needed for a fuller spatial picture of insect numbers are field data for harsh and kind environments similar to Andrewartha and Birch's hypothetical plots for *Austroicetes*. Ma (1958) presented data for *Locusta* during the last millennium based on composite records (Fig 1(a) in Zhang *et al.*, 2009) from southern China relating to global dynamics (Section **12.3.4**). Milne *et al.* (1965) give data for ten annual generations of *Tipula paludosa* (Section **3.2.1.2(f)**) on five farms in Northumberland, UK, that show density fluctuations of two orders of magnitude but little contrast. While data on the moth *Coleophora* (Randall, 1982) comprise only two generations, they are on an altitudinal gradient and reveal that different mortality factors operated at different levels (Section **12.3.4.3**). All examples are for herbivorous insects.

But from 1959 den Boer *et al.*, using pitfall traps and other means, studied the dynamics of predatory carabid beetles on Kralo Heath in the Netherlands. For *Pterostichus versicolor*, *P. lepidus*, *P. diligens*, *Amara lunicollis* and *Calathus melanocephalus*, annual populations generally varied by only an order of magnitude, and show an unusual lack of variation from year to year (den Boer, 1998). These beetles are generalists so perhaps their broad spectrum of food has this stabilizing effect. But data based on trapping a specialist predatory beetle, *Thanasimus dubius*, which eats bark beetles, show relatively small variation too (Reeve, 1997). In another specialized predatory group, the solitary wasps, mark/recapture studies also show stable adult numbers for several generations (Freeman, 1980; Taffe, 1983). Work on other beetles includes that of the USDA Forest Services, who have recorded fluctuations in the incidence of the pine beetle *Dendroctonus frontalis* from 1958. This results from aerial surveys of currently >40,000 km^2 of forest in east Texas, USA (Reeve *et al.*, 2002; Turchin, 2003), in which clumps of >10 infested trees were noted.

Good data of this type exist for a univoltine sawfly, *Euura lasiolepis*, which galls willow shoots in Arizona (Fig. 14.4 in Price *et al.*, 1998). Egg numbers over a 14-year period varied at about an order of magnitude higher at favourable (wet) sites than at unfavourable (dry) ones. In Jamaica, data for ~65 generations for the multivoltine gall midge *Asphondylia* in an altitudinal range of ~1000 m were recorded (Fig. 11.12; Freeman and Geoghagen, 1989). Flower galls contain a single egg, and all juvenile stages are passed in them, making sampling rapid and accurate (~10 sec/gall; Section **11.4.4**). The data, while similar to Andrewartha and Birch's *Austroicetes* data, show some differences. First, densities fluctuated by about an order of magnitude, as in Varley's winter moths, den Boer's carabid beetles and Price *et al.*'s sawflies. Second, density in the sub-optimal zone was as *high or higher* (mean 481 eggs/m^2) as that in the optimal zone (368/m^2), but there were ostensibly periodic extinctions. Third, hurricane Gilbert in September 1988, which caused immense havoc, did not cause extinction in the optimal zone, but as far as sampling showed, did so in the other zones. Finally, at the highest altitude the species was often absent and had a lower mean density (257/m^2) when present. Ungalled plants existed above the highest altitude for the midge, but were sparse. But these data show only half the picture since they relate only to patches. Because these are more numerous and hence closer together in the optimal zone, *relative to the landscape* the midges were much denser there than elsewhere (Section **12.3.4.1**). Ostensibly, re-established populations may or may not have been due to immigration.

We see that, apart from a bias for Lepidoptera and especially tortrix moths, there is also a bias for endopterygote insects. Although Clark and Dallwitz (1975) produced a fine data set for the Australian psyllid bug *Cardiaspina albitextura*, there is yet another bias for herbivores, doubtlessly because of their status as crop pests. Whittaker (1985), for another psyllid bug, the bivoltine *Strophingia ericae*, living on *Calluna* moor in the Pennines, found good evidence for cyclicity. This was probably due to an interaction between the annual cohorts. In conclusion, while long empirical data sets show bias, they provide good evidence of some sort of control.

The basic assumption in analysing time-series data is that there is correspondence between pattern and cause, namely that the observed levels and fluctuations are determined by ecological mechanisms. These fluctuations have an average period, a process order, topological features such as the shape of population peaks and troughs, and rates of increase and decline. In particular, one aims to elucidate the structure of density dependence (Turchin, 2003), which is assumed to exist. Another great advantage of these analyses, apart from economy of effort, is that they are applicable to all species, whereas life-table construction (Section **11.4**)

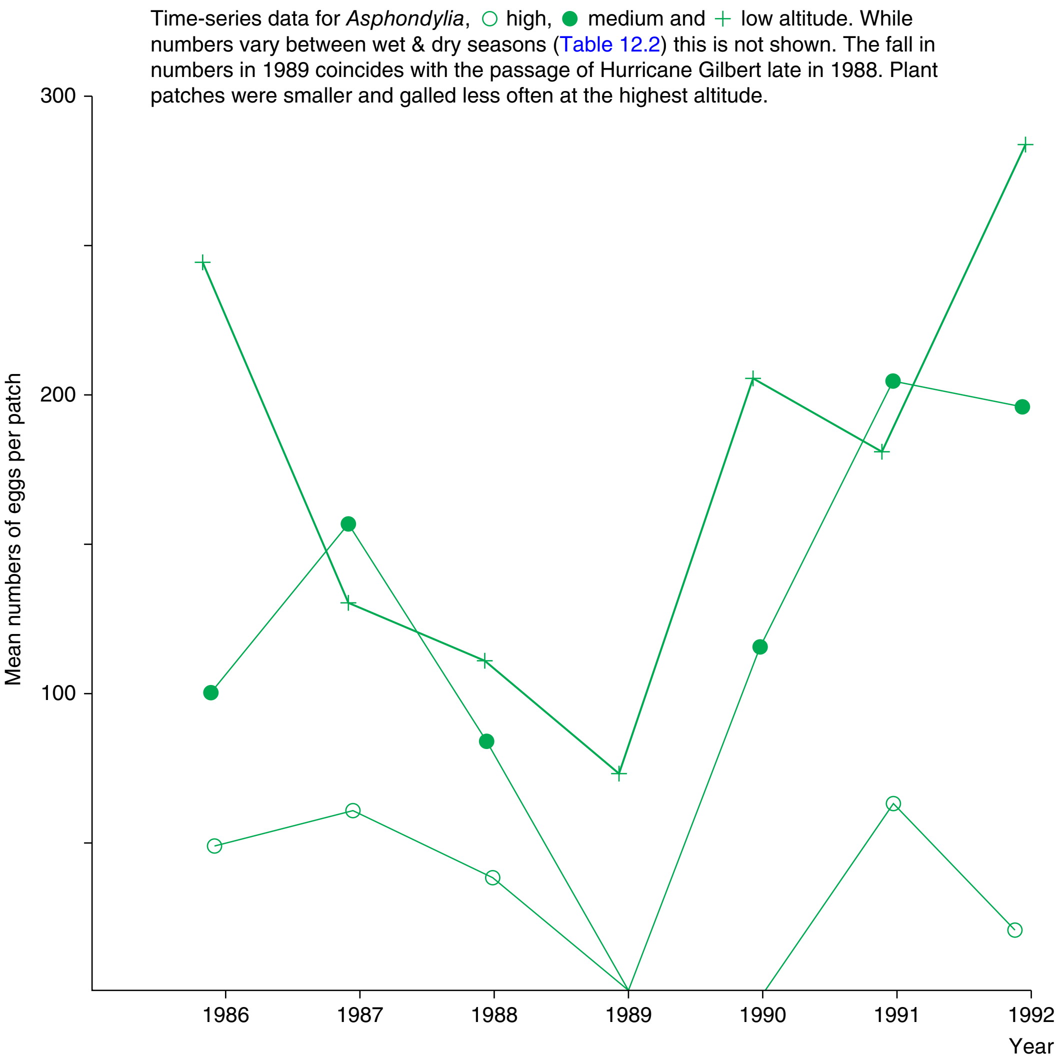


Fig. 11.12. Time-series data on the dynamics of the gall midge *Asphondylia boerhaavia* (see Freeman and Geoghagen, 1989). This midge lays single eggs in *Boerhavia* (Nyctaginaceae) flowers, a weedy relative of *Bougainvillea*. Conveniently, it produces (to us) conspicuous red galls in which a single egg is laid and all the developmental stages are passed. The data cover the period 1986 to 1992 and represent mean numbers of some 80 generations of eggs taken from >20 patches of food plant at each of three areas of increasing altitude in Jamaica.

is limited to cases where AF and the fate of eggs can be estimated with acceptable accuracy.

11.4 Life Tables: Value, Construction, Analyses and Limitations

11.4.1 General

Apart from direct deductive analysis of insect numbers with time (Sections **11.3** and **11.5**), population processes are understood best by using *life tables*. While noted earlier by Brownlee (1919), Fisher (1930) presented their theoretical background to the biological world as a prelude to his fundamental theory of natural selection. ‘Death tables’, however, would be more explicit and Fisher warned that they were only half the story: ‘The life table, although itself a very comprehensive statement, is still inadequate to express fully the relation between an organism and its environment; it concerns itself only with the chances or frequency of death, and not at all with reproduction'. He outlined a basic *reproduction table*, giving the expectation of births from adults surviving to a series of age intervals. As we noted, the logistic equation is concerned with a density-dependent rate of increase resulting from the balance of deaths *and births*. But in field studies, more attention has been given to the distribution of deaths than to that of births. Fisher combined data from both tables to derive m, his 'Malthusian parameter', defining rates of population increase when positive and of decrease when negative. This parameter can be estimated from field or laboratory data by the statistic r_m (Section **10.2.5.1**; Birch, 1948; Murray, 1989). Field fecundity (AF) is rarely zero but often greatly reduced from maximum potential fecundity achieved under ideal conditions. Nor is population mortality often zero, it is frequently >90% (Cornell and Hawkins, 1995) and can be total and virtually instantaneous in a catastrophe.

Pearl *et al*. (1941) used life tables to analyse survival in cultures of flour beetles, Deevey and Deevey (1945) used them for black widow spiders, and Deevey (1947) applied them in an interesting way to mortality of wild Dall sheep. These early tables did not identify or enumerate mortality, merely giving survival patterns and lumping causes together. They are *single-decrement tables*. More complete tables appeared when Morris and Miller (1954; Section **5.2.1.4(c)**) studied spruce budmoth dynamics in Canada. Several causes of mortality were estimated. They are *multiple-decrement tables* (Carey, 2001). Thus, proper life-table work is more onerous than that for time-series data, as magnitude, distribution and cause of mortality and natality are estimated, as Fisher foresaw and Morris and Miller developed. They usually document *top-down effects*, and occasionally the *lateral* influence of competition, but *bottom-up effects* (Section **10.1**) on births and deaths are also important. Deaths due to deficient food, the 'inadequate environment' (White, 1976) and plant resistance are mentioned rarely, but these, and also those due to genetic defects (Section **9.10**), no doubt occur regularly, often appearing under headings such as 'unknown causes'.

As with time series, the majority of tables have been compiled for herbivorous insects (Cornell and Hawkins, 1995). In contrast, few tables exist for predatory insects (but see Danks, 1971b; Freeman, 1973a, 1977, 1981a; Taffe and Ittyeipe, 1976; Ittyeipe and Taffe, 1982). For carabid beetles there are some partial data (e.g. van Dijk and den Boer, 1992). Apart from field life tables for such beasts, however, several laboratory studies on parasitoids exist, usually assessing their suitability for biocontrol. In such pre-release tests, workers are concerned to find species or strains that will have, hopefully, a high rate of increase in the field (Force and Messenger, 1964; Doury and Roja-Rousse, 1994; Pratissoli and Parra, 2000; Eliopoulos, 2006). But apart from field data for the eulophid wasp *Melittobia* (Freeman and Ittyeipe, 1993), the natural mortality and rate of dispersal of parasitoids are practical questions lacking answers. Much more fieldwork must be done as enemies are, of course, of direct interest for biological control (Section **11.4.4.1**).

Traditional life tables are of two classes (Southwood, 1978), while others have been developed. Firstly, *age-specific life tables* record the fate of a real cohort, usually a single generation of a given local population (Table 11.1). For endopterygotes, we start with the number of individuals entering the egg stage (l_x) and record the numbers dying in that stage (d_x) and from what factors (d_xF) (Morris and Miller, 1954), the remainder entering the first larval instar. This sequence continues through development, which can be divided into several larval instars, pupae and emerging adults. For exopterygotes there are only eggs, nymphs and adults. Secondly, *time-specific life tables* represent a time-section through a population with continuous reproduction, and hence overlapping generations, like a human one. This approach can be appropriate for stored product pests and some tropical insect populations.

A further class is the *retrospective life table* (Freeman, 1973a, 1976, 1981a; Freeman and Geoghagen, 1989; Freeman and Ittyeipe, 1993). At its simplest, it combines multi-generational data from one habitat, where *average effects* on births and deaths through time are estimated. It is naturally weighted, as dense generations contribute more to it than sparse ones do. Some workers have combined data from life tables, either for single species (LeRoux *et al*., 1963; Mukerji, 1971) or for many species (Cornell and Hawkins, 1995). A second, more informative type embraces spatio-temporal estimates: data from several generations and places within a species' distribution are combined. A global or metapopulation picture emerges that is

Table 11.1. A life table for third generation *Plutella xylostella* on cabbage in Ottawa.

x	*Lx*	*dxF*	*dx*	*100qx*
Eggs (N_1)	1154	Infertile	14	1.2
Young larvae	1140	Rain wash	536	47.0
Older larvae	604	*M. plutellae*	140	23.2
		Rain wash	77	12.7
			217	35.9
Prepupae	387	*D. insularis*	198	51.2
Pupae	189	*D. plutellae*	53	28.2
Adults	136	Sex ratio 0.401♀	27	19.9
Females ×2 (N_2)	109	Photoperiod	52.4	48.1
'Normal females' ×2	56.6	Adult mortality	48.1	85.0
Generation totals			1145.5	99.3

Expected eggs: 56.6/2 × 216 = 6113 $1 = N_3/ I_1 = 0.80$
Actual eggs: 918 (N_2) $S_G = N_2/N_1 = 0.094$

Young larvae are Harcourt's 'period 1' and older larvae his 'period 2'. *x,* age at sampling; l*x,* number alive at sampling; *dx,* number dying during this age interval; *dxF,* mortality factor causing *dx;* 100*qx,* % mortality. The number of females is doubled to keep balance in the table. In 'normal females' l*x* is the hypothetical number of females laying a full complement of eggs.

Modified from Harcourt, D.G. (1969) The development and use of life tables in the study of natural insect populations. *Annual Review of Entomology* 14, 175–196.

essentially *time independent*. This can be extended into a general *cyclic budget* (Section **11.4.3**). Such data have the same form as those for the Dall sheep (Deevey, 1947). When adequate, losses during redistribution and the pre-reproductive life of females can be estimated. Oddly, Mukerji (1971) and MacPhee *et al*. (1988) present similar 'summary' tables but do not comment on their *time-independent status* and their potential to yield extra critical information. Both Morris (1957) and LeRoux *et al*. (1963) present these 'mean' tables for diverse Canadian pests. Finally, in a meta-analysis (Peterson *et al*., 2009; Section **11.4.3**) combine data from several tables for a species to seek dynamic effects of indispensable mortality. But a further potential exists. In seasonal tropics (Section **2.2.3.2**) data for 'wet season dynamics' from several years can be compared to similar data for 'dry season dynamics', if the focal insect breeds in both seasons (Section **12.3.4.4(g)**).

11.4.2 Construction

The first of two recurrent problems with insect life tables is *accuracy of compilation* when estimating the l_x sequence (Harcourt, 1969). Accuracy is essential since when we go on to assess mortality we look at the difference between two successive estimates of number, both containing error. The problem is often acute for numbers entering larval and pupal stages. Apart from representativeness, an insidious problem arises due to the *variability of individuals. Even if they enter the egg stage at the same time, they do not develop in total synchrony*. Suppose we study a forest moth and wish to estimate the number entering the pupal stage in a given generation. If we took a sample, say from tree bark, when some individuals have pupated but most are still larvae, surely the sampled pupae have entered that stage but similar pupae may already have been eaten by birds and are lost without trace. Of course, we cannot simply add the living larvae since some of these will die *before* pupating. But if we wait to sample after all the larvae have pupated even more pupae will have died without trace. So negative bias creeps into our estimate, since *losses without trace* cannot be detected directly. This rationale applies to recruitment from any instar to the next. Not only juveniles killed by predators but also those parasitized may be lost. Apart from parasitism, parasitoids often kill hosts without laying an egg in them (Thompson and Parker, 1928a; Jervis and Kidd, 1986; Berryman, 1996). So parasitism estimated by rearing or dissection will contain a negative bias of unknown size (van Driesche, 1983; van Driesche *et al*., 1991; Werren *et al*., 1992; Kidd and Jervis, 1996). Another complication is that there may be more than one parasitoid generation in a single host generation (Simmonds, 1948). Various computational methods, requiring several sequential samples, can reduce these problems (Southwood, 1978; van Driesche *et al.*, 1991; Bellows *et al.*, 1992). But error accrues in the estimates of l_x, leading to greater error in the estimate of mortality within a stage (d_x). Work the Rothamsted statistician Reg Wimble and I did in the 1960s led us to believe these errors would be material. Reg died tragically at about this time and publication was impossible.

So it is to George Varley's credit that he divined a way of avoiding these grave difficulties by using *traces*. He studied tephritid flies (Varley, 1947) as their oviposition caused growth of a gall, a rather permanent artefact, facilitating mortality estimates (Varley, personal communication, 1963). This principle was used later to investigate predation by small mammals on sawfly cocoons (Holling, 1959a). Traces are especially useful in developing retrospective tables, but have often been used in traditional tables too. Straw (1991), working on gall flies in Monk's Wood (UK), extended Varley's trace concept. Bark beetles leave life-history traces in wood (Beaver, 1966, 1967; Berryman, 1973) in temperate situations and in the tropics (Beaver, 1979; Garraway and Freeman, 1981, 1990). Life tables for cerambycid beetles in wood have been constructed (Grimble and Knight, 1970, 1971; Togashi, 1990). Lu (in Liebhold and Tobin, 2008) extended trace methods for such beetles by linking them to dendrology, thus effectively extending sampling through time.

The dynamics of solitary wasps and bees that make long-lasting mud cells have also been studied (Danks, 1971a and b; Freeman, 1973a, 1976, 1977, 1981a; Smith 1979; Jayasingh and Freeman, 1980; Watmough, 1983). Further examples of trace methods are on gall midges (Redfern and Cameron, 1978; Freeman and Geoghagen, 1989; Redfern and Hunter, 2005), gall wasps (Hails and Crawley, 1992), some larval Lepidoptera (Courtney and Duggan, 1983; Garraway *et al.*, 2008), leaf mining flies and moths (Martin, 1956; Heads and Lawton, 1983; Kato, 1985; Freeman and Smith, 1990; Mopper *et al.*, 1995; Brewer and Gaston, 2003; Klug *et al.*, 2008), and a eulophid wasp within solitary wasp cells (Freeman and Ittyeipe, 1993). The detailed artefacts, head capsules, cocoons and puparial cases (Mukerji, 1971) and other traces left by the focal insect and its enemies, *provide direct, unbiased estimates of the* $\mathrm{l_x}$, *and often the* $\mathrm{d_x}$. They occur in a range of endophytic insects, and those that extend their phenotype (Dawkins, 1982; Turner, 2000) in the shape of semi-permanent egg cases, webs and protective cells. Mud cells are also valuable to study distribution (Freeman, 1977, 1982). Although the wasps that make them live only a few weeks, the cells remain *in situ* for several years, multiplying the effective density by at least an order of magnitude.

In life-table work, traces allow more accurate estimates than those from direct sampling as they can provide a record of entries into every stage of the focal species and often the cause of death. Caterpillars leave semi-permanent traces when they munch the leaves of specific food plants, making them easier to find, estimate their size and give some idea of their mortality (Pollard, 1979; Garraway *et al.*, 2008). For our forest moths, if cocoons were not removed from the bark, say by birds, they would provide an accurate trace of each individual entering the pre-pupal or pupal stage. Avian predation has been estimated from torn-open sawfly cocoons (Holling, 1959b), while diagnostic exit holes made by adults provide a good estimate of emergence. Of course, representativeness is a separate issue, and we recall from Section **10.1** that life tables record only proximate causes of mortality; less proximate ones, such as temperature, do not appear. But without traces, even if all individuals are in the same stage, as in diapause, estimates will still be negatively biased to an unknown degree because of mortality before sampling can begin (Harcourt, 1969).

In trace work, the larval instar dying can be identified by measuring head capsules of the cadavers and the numbers entering a stage estimated by counting shed capsules of the previous instar. Larval wasps and weevils generally have three instars whose head capsules have different sizes. When forest caterpillars shed them at ecdysis, they can be collected as they rain down from above. With this ingenious method, Higashiura (1987) studied *Lymantria* on Hokkaido, Japan. If several traps are randomly allocated to the study area to collect capsules for a complete generation, one can estimate successive larval densities relative to the forest floor, a true density estimate (Sections **9.3** and **10.1**). When integrated, these form the l_x column of a life table. The unknowns, of course, are the d_x factors, which should be estimated separately; however, the l_x column would be accurate. The method could be adapted to study the dynamics of some foliar pests on orchard and field crops and would be better than using the less-accurate computational methods in Southwood (1978).

Some workers seem not to understand these principles, *although they have been pointed out* *repeatedly* (Simmonds, 1948; Richards and Waloff, 1954; Dempster, 1961; Harcourt, 1969; Freeman, 1976; Birley, 1977; van Driesche, 1983; Manly, 1990; van Driesche *et al*., 1991; Bellows *et al*., 1992; Southwood and Henderson, 2000; Turchin, 2003). *While numbers present on a given day can be estimated with relative ease, the total numbers entering a specified instar cannot*. An example and many references are given here, since this understanding is crucial for the accurate study of insect pest dynamics. Thus, MacPhee *et al.* (1988), working on winter moths in Canadian apple orchards, and in an otherwise informative long-term study, estimated the numbers of first and second instar larvae (combined) by the higher of two direct counts made per leaf cluster. Counts of large larvae (fourth and fifth instars combined) were made similarly, before pupation started. Numbers of young larvae entering this stage, estimated as intensity (Section **9.3**) per cluster, are inaccurate since as the authors state, not all eggs had hatched on the sampling date and because some mortality and emigration of early hatched larvae had occurred before sampling. This gave a negative bias to the estimate, although larvae arriving on silken threads from other trees may have partly offset this (Holliday, 1977, 1985). Sivapragasam *et al.* (1988), working on life tables for *Plutella* in Honshu, did not make this error. van Driesche *et al.* (1991) review three basic methods by which this problem can be reduced: stage frequency analysis, estimation of recruitment to a stage, and death rate analysis. But nothing is as accurate as trace methods, and my guess is that it never will be.

Field estimates of AF are often difficult (Richards, 1961; Myers, 1988). MacPhee *et al.* (1988) sampled females ascending trees and dissected them to estimate fecundity. But the proportion of them that ascended trees, as East (1974) estimated, and the proportion of these that survived to oviposit or died while laying eggs (see Betts, 1955; Section **5.2.1.4(g)**) is unknown. So accuracy of the estimates of AF was also compromised. Improvements by studying female behaviour, collecting spent females on the trees and watching oviposition in an insectary were possible. Fortunately, since numbers varied by almost two orders of magnitude in a generation the main population trends will still be valid.

The other problem with life tables, as Fisher (1930) noted, is that the influence of variations in natality, often due to several causes (Section **11.2.3**), may be ignored. With poor or insufficient food, adult females will be smaller and less fecund (Section **10.2.5.2**). For herbivores, plant resistance in its various forms (Section **2.4.2**) can do the same (Mopper *et al*., 1995). Higher than normal temperatures during development may also result in smaller adults (Section **10.2.5.3**). Infertility, which may result from low population density and/or bad weather, is a further factor. Bad weather during oviposition reduces AF directly (Sections **10.2.5.3** and **10.2.5.4**). Berryman (1973) includes estimates of reduced natality in his analysis of *Scolytus* dynamics. Freeman (1977, 1981a) for *Sceliphron assimile* and *Trypoxylon palliditarse,* respectively (Section **11.4.3**), also estimated variation in natality.

We now give an example of how an age-specific life table (Harcourt, 1969) and a retrospective one (Freeman and Geoghagen, 1989) are constructed. Harcourt's table for *Plutella xylostella* in Ottawa is for a single autumn generation of the moth, one that is 'typical' of many such tables over several generations. He introduces the concept of a *time-independent table* without saying so! It is well based (see Table 11.1). The egg count is at the end of egg laying and infertility is estimated by rearing a large sample. But were any lost without trace? The number entering the first larval instar ('period 1') is that of eggs that hatch. The next estimate is the number of cocoons spun by mature larvae. They are never lost or destroyed and so are good traces. Working back, late sampling of large larvae and rearing *Microplitis* parasitoids from them estimates numbers entering his 'period 2' larvae. The estimate of prepupae in cocoons killed by *Diadegma insularis* is from field cage results. Again, pupal numbers are found by collecting them after pupation in the field is complete and rearing samples to estimate the number killed by *Diadromus plutellae*. All unparasitized pupae hatch, so estimates of adult emergence are sound. But females laying the next generation of eggs are in a minority (0.401). The AF estimate is 112. Harcourt then, very properly, draws attention to the inaccuracies expected due to redistribution, which in this vagrant moth (Section **5.2.1.4(a)**) may be considerable.

For *Asphondylia boerhaaviae,* in Jamaica we find the advantages of trace methods. These midges deposit single eggs in *Boerhavia* flowers and a big red gall develops rapidly, giving a long-lasting trace of entry into the egg stage (Table 11.2). Although caterpillars eat a few galls, this too leaves a trace.

Table 11.2. A life table for a single generation of the gall midge *Asphondylia boerhaaviae* in a single patch of *Boerhavia diffusa*, Mona, Jamaica, 31 August 1989. M_a, M_r and M_i are apparent, real and indispensable mortalities, respectively.
No. of eggs sampled = 296 Total galls in patch = 1184
Density/m^2 = 538

	l_x	d_x	%M_a	%M_r	%M_i
No. entering larvae 1+2	= 296				
Competition by Galeopsomyia		= 33	11.1	11.1	2.4
Total d_x =		33			
No. entering larvae 3	= 263				
Parasitism by *Heterolaccus*		= 3			
Parasitism by *Calorileya*		= 116			
Parasitism by *Eurytoma*		= 34			
Death from failed parasitism		= 7			
Caterpillar predation		= 2			
Endogenous mortality		= 15			
Total d_x =		177	67.3	59.8	40.2
No. pupated	= 86				
Parasitism by *Heterolaccus*		= 14			
Parasitism by *Calorileya*		= 8			
Parasitism by *Torymus*		= 4			
Endogenous mortality		= 2			
Total d_x =		28	32.6	9.5	9.5
No. of adults emerged = 58					
% Emergence = 19.6					

Boerhavia patches bear ~100–1000 galls, while several generations of the midge are passed in them. At emergence a pupal case may remain thrust through the gall. If lost, its permanent trace has diagnostic projecting plant fragments. Samples are taken when the large majority of midges have died or emerged. In the former, artefacts in intact galls allow direct counts of the l_x, d_xF and d_x, and identification of the parasitoids. The d_xF term 'endogenous mortality' refers to deaths within the galls, some of which may be due to genetic causes. Hudson's correction is applied to the data to compensate for errors due to live immature midges, the l_x column. This table represents 46,750 galls in ~70 generations and 39 sites in Jamaica, so estimating the midge's average population dynamics (time independent) in the island. The result is a *global life table* (Section **11.4.3**), at least as far as Jamaica is concerned.

11.4.3 Analysis

Standard information can be extracted from life tables (see Table 11.1). *Apparent mortality* is the number of individuals dying in any stage as a proportion of the number entering that stage. *Real mortality* is the number dying in any stage as a proportion of the number of eggs in the sample, a distinction noted by Thompson (1929). Real mortalities may be added, which is appropriate when, for example, a parasitoid kills both larvae and pupae. *Indispensable* (= *irreplaceable*) *mortality*, also noted by Thompson, is defined by Southwood (1978) as 'that part of the generation mortality that would not occur, should the mortality factor in question be removed from the life system, after allowance is made for the action of subsequent mortality factors'. Finally, there is the *marginal attack rate,* the proportion of individuals entering a stage that would be attacked by a mortality factor if it acted alone instead of in combination with other such factors (Royama, 1981). When these factors act alone they are equivalent to apparent mortalities. When two or more factors act together, each is devalued by the action of the other(s), and so less than the apparent mortality (Bellows *et al.*, 1992; Peterson *et al.*, 2009). Thus mortality factors are not a single 'grim reaper', but act like a pack of 'little devils' (Kannisto, 1991, in Carey, 2001): one devil can largely replace another.

As we have seen, life tables record the actual cause of death, namely the proximate mortality factor (Sections **10.2.1** and **11.4.2**). For example, temperature may permit, or not permit, an aphidiine wasp to parasitize and probably kill an aphid. But temperature, although critical to the interaction, does not appear in the table.

Another problem is the *statistical validity of interpretation*. When age-specific life tables have been prepared for a given local population through several generations (ideally eight to ten, or more), further analyses can be made. The first move is to see how a given mortality factor relates to density, namely, is it density dependent or not? (Section **10.2.3.7**). This is revealed by correlation and regression analyses, preferably after converting the data into *k* values. These were proposed by Haldane (1949), used by Morris (1959) and further developed between 1960 and 1975 by Varley's Oxford Group. They are derived by converting the l_x values into $\log_{10}$ values (Varley and Gradwell, 1960). The successive differences between these logs are the *k* values representing the magnitude of mortality at each interval, so that:

$$K = k_1 + k_2 + \ldots k_i$$

When several sequential generations have been charted (**Fig. 11.13**), we see how variation in each *k* relates to *K*, the total mortality. While a key factor may be obvious by inspection, Podoler and Rogers (1975) give a quantitative method for finding it. Kidd and Jervis (1996) give detailed information on life tables and *k* values. Over 400 papers using this analysis show the method's popularity.

But statistical violations and other problems occur in the method (Royama, 1981, 1992, 1996; Dempster, 1983; Bellows *et al*., 1992; Peterson *et al*., 2009). Firstly, since the *k* values are calculated from the estimates of density, they are not independent of them, a necessary condition for valid correlation and regression (Bailey, 1994). There are other pitfalls when using such analyses, especially of ratios and indices (Jackson and Somers, 1991). *K*-factor analysis also assumes that the mortality factors operate sequentially, not concurrently. In cinnabar moth dynamics, if the order in which starvation and predation of the larvae are reversed, the one that appeared to be the key factor is also reversed (Putnam and Wratten, 1984). Ominously, an arbitrary division of stages in the life table can create a significant key factor (Royama, 1996). Problems may also arise from serial correlations found in time series, and from the fact that the analysis overlooks the potential importance of a factor that has little *variation* over time.

While key-factor analysis produces *patterns* of population fluctuation and of associated mortality factors, it does not discover their cause. 'The essence of the study of population dynamics is to analyse an observed process into major components and then to synthesize them to recreate the dynamics' (Royama, 1996). He suggests a simple alternative method in which the $\log_{10}$ survival rates during the juvenile stages, H_1, $H_2 \ldots H_n$, the $\log_{10}$ recruitment rate H_r, the $\log_{10}$ rate of change between generations *R*, and the $\log_{10}$ egg density *X*, are tabulated for each generation. These parameters form the relationship:

$$R = H_1 + H_2 + \ldots H_n + H_\mathrm{r} = H_\mathrm{g} + H_r$$

where H_g is the generation survival rate. To be comprehensive, H_r must include eggs laid by any immigrant females. Graphical analysis then permits a better understanding of the regulatory process. Royama concludes: 'We must look into a more comprehensive method, or system of methods, to analyse each set of population process data …'. Recently, other complex methods avoiding the pitfalls of key-factor analysis have been developed, but their details are outside the scope of this book. Briefly, Carey (1989) introduces multiple-decrement life tables, which record: (i) the age or stage distribution of death from different causes acting together; (ii) the chance that a new-born individual will die after a given period from a specified cause; and (iii) how the mortality pattern might change if given factors were removed? Brown *et al.* (1993) develop the method of '*structural accounting of the variance of demographic change*', applying it to red deer population, which may be more appropriate for vertebrates. Then Sibly and Smith (1998) proposed the method of *lambda contribution analysis*, which, like Royama's method, includes the effects of births as well as deaths. It differs from the traditional approach because it statistically weights the *k* values according to their influence on the rate of population growth and hence population change. Yamamura (1999) presents a key-factor/key-stage method of analysis, while Peterson *et al.* (2009) have re-analysed some existing tables for herbivorous insects using the multiple-decrement method. Significant errors accrue if factors acting together are not treated in this way.

Although life tables have been applied to field populations for some 70 years, their relationship to what could be called 'average' or 'normal' dynamics of an entire species has not been sought rigorously. But this link has been tacitly assumed (Morris and Miller, 1954), mooted in the generally direct correlation between AF and juvenile mortality (Price, T., 1997) and is implicit in LHS. A step towards unification was the development of a *time-independent life table*, a modification of Varley *et al.*'s (1973) population budget (Freeman, 1976). According to the breadth of its sample base, it seeks the dynamics typical of the species so quantifying LHS. For accurate application a constant mean

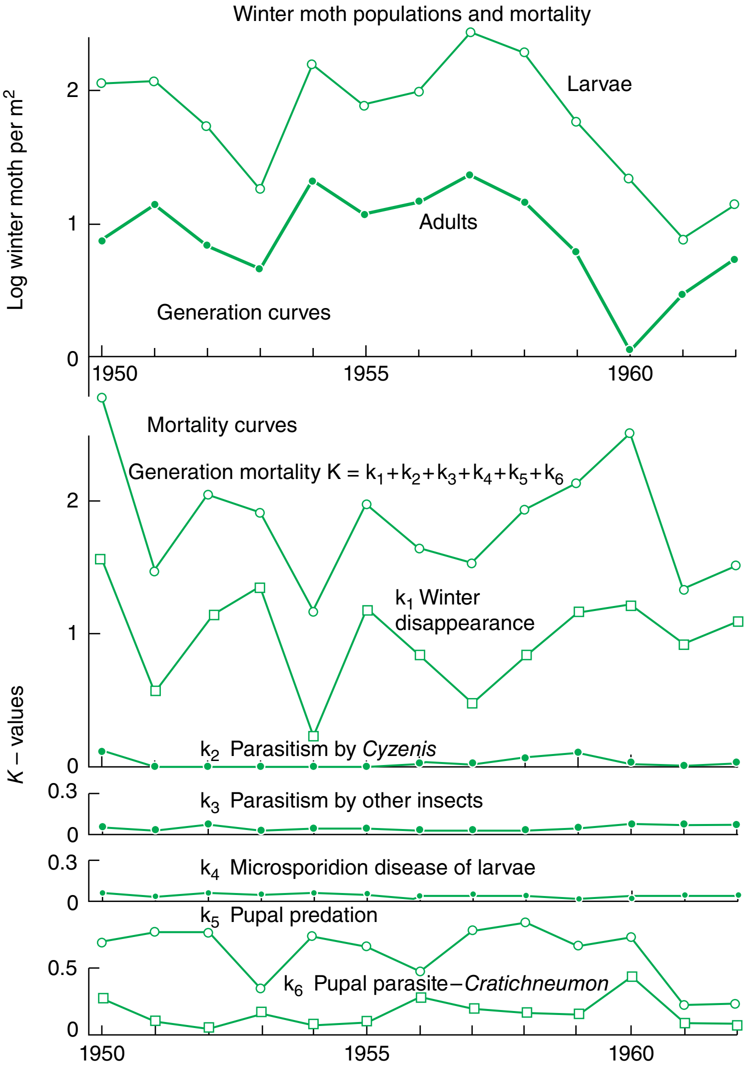


Fig. 11.13. Varley's *K*-value analysis. The $\log_{10}$ values describe the numerical change to a local population for a single generation (they are nothing to do with *K*, the carrying capacity, in Verhulst's logistic). When several sequential generations have been charted in this way, the magnitudes of *K* and k_1 to k_6 are plotted on the number of generations sampled, giving a graph of how the variation in each *k* relates to *K*. The factor making the greatest contribution to population change is called the 'key factor'. From: Varley, G.C., Gradwell, G.R. *et al*. (1973) *Insect Population Ecology: an Analytical Approach*. Oxford: Blackwell. Reproduced with permission.

density for a long and representative period is needed. Over such time, births and deaths are virtually equal (Nicholson, 1958; Maynard Smith, 1983b).

While retrospective tables tell us little about time-dependent control between generations, they do provide valid estimates of the overall form of the mortality curve (Taffe, 1983; Cornell and Hawkins, 1995) and so the cause-of-death probabilities and spatial variation of mean natality and mortality (Freeman, 1973a, 1976, 1981a). More importantly, when extended to form a *cyclic budget*, they estimate the overall *magnitude of population losses incurred during dispersal and migration*, as Danks (1971b) first suggested, a feature lacking and often ignored or confounded in insect life tables (Hill *et al.*, 1996). But it is practical to get adequate data for a retrospective table from a metapopulation only when it provides long-lasting traces of births and deaths. While this limits the number of species that can be investigated, suitable cases occur in several insect orders, and indeed in other animal groups. The Dall sheep skulls could be aged and sometimes the cause of death, often by wolves, identified (Deevey, 1947). They represent deaths over 4–10 years or more. So such tables elucidate spatial effects, but not temporal changes, in an extensive population or metapopulation. Real, apparent and indispensable mortalities can be estimated validly from them, but again, they gain accuracy when used for a population through more and more generations.

To give an explanatory case, apart from Dall sheep, this form of table can display long-term data collected from the wasp *Sceliphron assimile* (Freeman, 1973a). Its mud cells last many years and since the life cycle is only ~45 days, according to conditions, they represent as many as 50 sequential generations. One egg is laid per cell, so a sample of cells represents a sample of eggs laid in the past. If the progeny become adults they chew out of the cell leaving a characteristic exit trace, so breeding success at a locality for several years can be estimated. Years of abundance contribute more to the sample than years of scarcity; so they are naturally weighted. When juvenile wasps die they are 'mummified' in the cells, often with traces of mortality agents. Although females may make more than one nest, mean nest size estimates minimum AF. Sampling the number of nests that a female makes allows an unbiased estimate of AF (Freeman, 1980).

To calculate metapopulation or global losses during redistribution, data from many generations and locations are incorporated in a general cyclic budget (Freeman, 1976; Fig. 11.14), a time-independent figure that takes mean AF and sex ratio into account. For several species these losses, which also include failure to find resources for the next generation, are the largest item in the budget. Its accuracy depends upon its spatio-temporal representativeness, and on the assumption that the

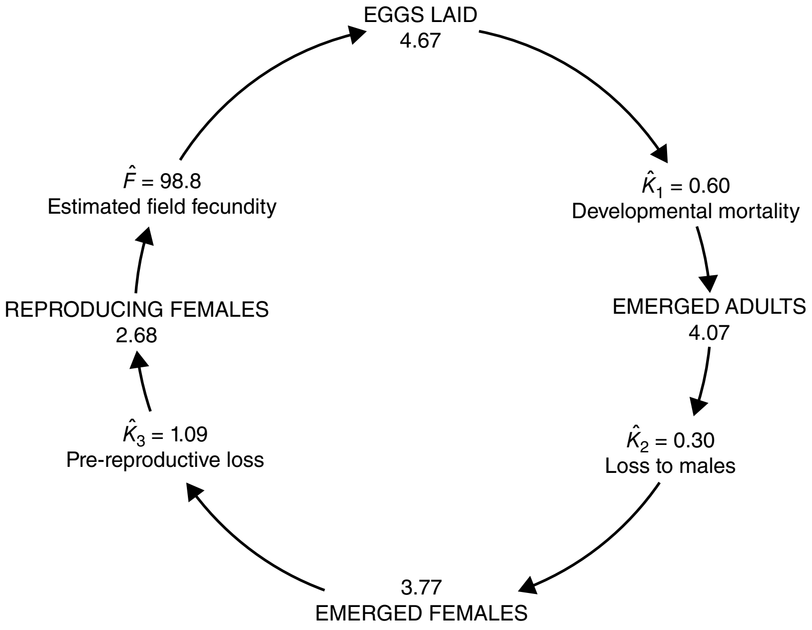


Fig. 11.14. A cyclic budget for *Asphondylia boerhaaviae* in Jamaica using logarithmic values at each stage. $\hat{k}_1$ = juvenile mortality, $\hat{k}_2$ = loss to males, $\hat{k}_3$ = interpolated estimate of the pre-reproductive mortality of adult females, $\hat{F}$ = estimated field fecundity. This budget is based on numbers sampled at 39 sites throughout Jamaica. Under steady-state conditions, $\hat{F} = \hat{k}_1 + \hat{k}_2 + \hat{k}_3$. We see that losses of adult females before they can reproduce is a major feature of mortality. From Freeman and Mulder, 2018 (Submitted). The original budget, for *Sceliphron*, is in: Freeman, B.E. (1976) A spatial approach to insect population dynamics. *Nature* 260, 240–241.

population fluctuates about a fixed mean level (Fisher, 1922; Nicholson, 1933, 1958; Stern *et al*., 1959). Then, the excess of natality over mortality estimates losses during redistribution and the period of ovarian maturation, should there be one (Section **10.2.5.1**). The value of this approach is considered further in Section **11.4.4.3** in relation to metapopulations.

11.4.4 Results: What do life tables tell us about population dynamics?

11.4.4.1 General introduction

Most data from which age-specific *field life tables* have been constructed relate to patches (Section **12.2**). Sampling larger areas is normally too onerous unless trace methods are used or extensive skilled manpower available (Morris, 1963; Section **11.4.4.3**). The information obtained relates only to the spatial level sampled. When it is analysed to seek dynamical patterns, three questions should be in mind: (i) Are the population units in the sample patches representative? (ii) What is the effect of variation in natality? (iii) Have the redistributional and pre-reproductive losses been estimated?

Having packaged data in a life table various analyses can be made. The first is to assess the magnitude and distribution of mortality in a generation. Usually most individuals die before reaching adulthood, there being a general, but not universal, direct relationship between fecundity and juvenile mortality (Cornell and Hawkins, 1995; Price, P.W., 1997). Some species like *Melittobia australica*, *Eupelmus orientalis* and *Dacus oleae*, however, have high AF but low mortality (Section **10.2.5.1**), an effect most likely to occur when density-dependent mortality is inoperative, weak or significant only at high density. In *Chrysonotomyia*, a eulophid parasitoid of *Papilio homerus* eggs, only 6.10 +/− 0.02% juvenile mortality is recorded (Garraway *et al*., 2008). Recall that most populations are sparse (Section **9.4**) and limited by other means. Juvenile mortality can occur in three patterns although there is variation: high at the start, high at the end, or at a steady rate. As insects develop in several instars, a corresponding step-like pattern of mortality superimposed on these trends often occurs. Cornell and Hawkins (1995, see Figs 1 and 2 in their article) give selected data sets for 124 herbivorous, endopterygote species. While all patterns occur, the average trend (see Fig. 3B in their article) is a decremental curve with only 5–10% survivorship to the emerged adult (Fig. 11.15). Even so, where AF is >100 there is plenty of room for pre-reproductive adult mortality to occur even when numbers are maintained or increase.

The temporal distribution, intensity and causes of death in juvenile herbivorous insects (see Fig. 4 in Cornell and Hawkins, 1995; Fig. 11.16) are of central interest. Harsh weather, largely heavy rain and extreme cold, and plant defences have the greatest effects on eggs and young larvae. But enemies are the major cause of death generally, increasing to ~60% in late larvae and pupae. Leaf miners are very susceptible to parasitoids. Overall, these beasts kill more victims than predators do, being very active in temperate regions (Hawkins *et al*., 1997). In *Rhopalomyia* (Cecidomyiidae) parasitism causes >80% juvenile mortality (Briggs and Latto, 2000). Predators and pathogens are especially important in the tropics, where pupae are very vulnerable. All forms of competition *play a minor quantitative role everywhere*. Unexpectedly, enemies kill similar proportions of herbivores in natural and cultivated habitats, while native and exotic species suffer similar levels of attrition. Intrinsic factors largely affect eggs and pupae. These are immobile stages in which major structural changes occur, so perhaps genetic defects are involved. While physical factors cause only ~10% of the mortality, unknown factors comprise ~20%, and may well include weather and, again, genetic defects. But as we have seen only proximate mortality factors are recorded. Naturally, weather influences the course of enemy action, as with aphid parasitoids (Section **10.2.1** and **11.2.2.4**). Hawkins and colleagues also found that exophytic herbivores are more susceptible to pathogens than their endophytic counterparts.

Field life tables for predators and parasitoids, when sufficiently addressed, will likely be similarly diverse. Extensive data exist only for solitary wasps (Danks, 1971b; Freeman, 1973a, 1977, 1981a, 1982; Freeman and Taffe, 1974; Freeman and Jayasingh, 1975a; Smith, 1979; Taffe and Ittyeipe, 1976; Taffe, 1979; Jayasingh and Freeman, 1980; Muthukrishnan *et al*., 1983). These beasts have high maternal investment and predatory efficiency, low AF and juvenile mortality. By contrast, carabid beetles scatter eggs widely and while AF may be low in genera such as *Harpalus*, it may be much higher in *Pterostichus* under good field conditions. Their larvae suffer great attrition from adverse

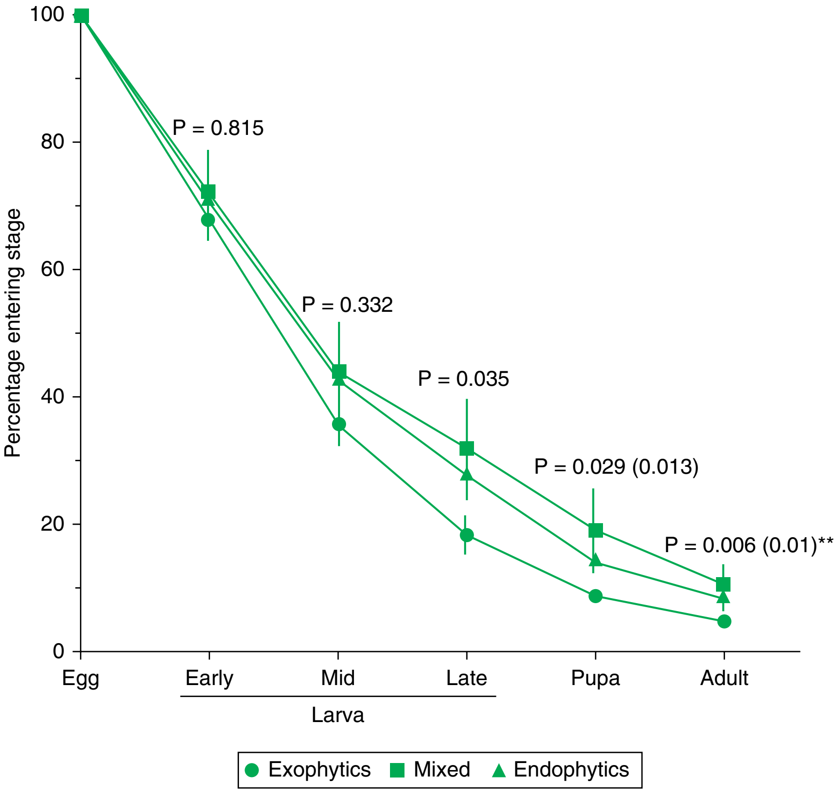


Fig. 11.15. Survivorship in three categories of herbivorous insects. Adapted from Cornell, H.V. and Hawkins, B.A. (1995) Survival patterns and mortality sources of herbivorous insects – some demographic trends. *The American Naturalist* 145, 563–593. Fig. 3b. Reproduced with permission.

physical conditions in the soil, especially flooding, while prey capture is inefficient (Luff, 1982; van Dijk, 1994; den Boer, 1998). Tiger beetles also have reduced RS when food is short (Pearson and Knisley, 1985). Little hard field life-table data exist for other predatory groups such as ladybirds (Hodek *et al.*, 2012), although laboratory studies are common (Lanzoni *et al.*, 2004). Lacewings, Heteroptera and Syrphinae are similarly little known.

The great gap in our knowledge is scarcity of *field life tables for parasitoids*. To understand their natural dynamics and hence their deployment in biocontrol, data are needed on fecundity, mortality, sex ratio and redistributional losses. Excepting work on two tachinid flies: *Cyzenis albicans* (Hassell, 1969) and *Bessa harveyi* (Valovage and Kulman, 1986) and my work with Ittyeipe on *Melittobia* (Freeman and Ittyeipe, 1993), little is known (Force, 1974; Cronin and Reeve, 2005). Laboratory studies exist (e.g. Nikam and Pawar, 1993; Doury and Rojas-Rousse, 1994; Eliopoulos, 2006; Kalyebi *et al.*, 2006; Abe *et al.*, 2009). *More field data are needed*. When trace data can be obtained for hosts, *they may also be had for their parasitoids*. Some incomplete results have been obtained (Varley, 1941; Freeman and Ittyeipe, 1976; Hardy *et al.*, 1998). In *Torymus* (Torymidae), the host density of the gall midge *Taxomyia* apparently determines that of the parasitoid (Cameron and Redfern, 1978). Recent fieldwork has employed genetic structure as a proxy for dispersive tendency (Lei and Hanski, 1997; Kankare and van Nouhuys, 2005; Anton *et al.*, 2007; van Nouhuys and Laine, 2008; Nyabuga *et al.*, 2010). Finally, the dynamics of hyperparasitoids are unknown. However, these and parasitoids die as eggs or larvae if their hosts die of other causes.

While Hassell's paper contains no life table, it does have estimates of the basic parameters necessary to unravel the natural dynamics of *Cyzenis*,

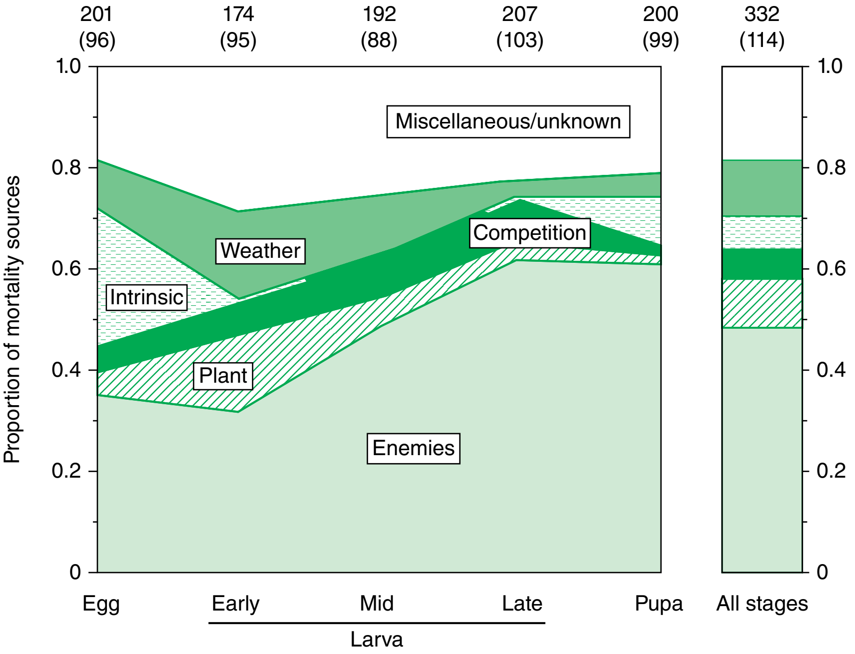


Fig. 11.16. Survival patterns and sources of mortality in some herbivorous insects. From Cornell, H.V. and Hawkins, B.A. (1995) *The American Naturalist* 145, 563–593, Fig. 4. Reproduced with permission.

which is specific to the winter moth. Females scatter hundreds of eggs on foliage the larval host has chewed. But few eggs survive as only large larvae can swallow them intact and there is often asynchrony between oviposition and host presence. Then, as above, the successful young parasitoid is subject to the considerable mortality of its host due to causes other than parasitism, for example avian predation, especially by titmice (Betts, 1955). Finally, what is probably a generalist hyperparasitoid, *Phygadeuon dumetorum*, attacks *Cyzenis* itself (Varley *et al*., 1973).

Bessa harveyi afflicts several forest sawflies including *Pristiphora erichsonii* and *Pikonema alaskensis*. So, unlike *Cyzenis* it is a multi-host species (Turnock, 1978; Valovage and Kulman, 1986; Section **5.2.1.3**(e)). The eggs are laid directly on large larvae, and again unlike *Cyzenis*, AF is low at ~30–50. Young larvae are endoparasitoids, overwinter in their host, and of course die if their host dies. A major unknown for both tachinid species, indeed all endoparasitoids, is, 'does its parasitism affect mortality from other causes?' In one such case, when two *Cephus* larvae contest the limited space of a wheat stem (Section **9.8**), if one is parasitized it invariable loses. The main physical mortality factors of *Bessa* include flooding, desiccation and freezing. Biotic factors are infertility, superparasitism causing competition, and encapsulation by the host. The latter may be influenced by the host's food plant (Section **10.2.3.8**).

In great contrast, *Melittobia australica* lays several hundred eggs on the integument of a single wasp or bee larva or prepupa enclosed in its protective cell. As in *B. harveyi,* there are several host species. Most of the modest (~25%) juvenile mortality is due to density-dependent competition between the sibling larvae for space, sometimes as a result of superparasitism. Hassell (1969) did not estimate the sex ratio in *Cyzenis*, but it is probably ~1:1, as in *B. harveyi.* In *M. australica*, however, as in other congeneric species (Schmieder, 1933; Abe *et al*., 2009), it is ~20:1, that is, highly female biased. In another ectoparasitic, eulophid wasp (*Colpoclypeus florus*) the sex ratio, as expected (Hamilton, 1967), is increasingly spanandrous in larger clutches (Hardy *et al*., 1998). These vary from ~10–50 eggs according to host size (*Adoxophyes orana*; Section **13.3.3.2**). Females can lay more than one clutch. Some 40% of these wasps reach adulthood, but mortality is *density independent*. In some small clutches no males survive and the sisters remain sterile.

The tropical eupelmid wasp *Eupelmus orientalis* is a *solitary* ectoparasitoid of juvenile bruchid beetles infesting stored cowpeas. The *laboratory* estimate of AF is 220 and that for juvenile mortality only 39%, intra-brood competition as in *Melittobia* being the main factor (Doury and Rojas-Rousse, 1994). In *Chrysonotomyia* spp., a eulophid egg parasitoid of *Papilio homerus*, numbers per host can be counted from the wasp's oviposition scars left on the chorion, another trace method (Garraway *et al.*, 2008; Section **11.4.2**). While unisexual broods usually occur in each egg, the overall sex ratio is mildly female biased (0.63 ± 0.04 female). Juvenile mortality is merely 6.10 ± 0.02% (Section **11.4.4.1**), and while this does not include some eggs that are lost to ant and avian predation, great mortality of migrant females is still expected on the basis of stable numbers (Section **11.4.3**). In *C. florus* and *E. orientalis,* migratory losses may be considerable too.

Even with this minuscule sample, we see that great dynamic diversity of parasitoids exists, especially because of their many modes of reproduction. Egg parasitoids attack hosts in their most numerous stage, a stage having little immunity. They also avoid later host mortality. Conversely, parasitoids of pupae and adults attack the least numerous host stages, but avoid their earlier mortality. With egg scatterers, unlike those that oviposit in the host, a huge mortality of eggs ensues outside the host. The consequences of superparasitism must also be remembered. Early comparative work by Varley (1941) on five chalcidoid parasitoids of *Urophora* showed that this factor varies greatly between species. When parasitoids develop gregariously, female-biased sex ratios often result, as in *Colpoclypeus*, *Melittobia, Chrysonotomyia* and many *Apanteles* (s.l.), but there are several complicating mechanisms (Waage, 1986). In aphids, parasitoids may be deterred by secondary symbionts (Oliver *et al.*, 2008). For parasitoids of herbivores, food plant quality may affect juvenile mortality (Ohsaki and Sato, 1994; Singer and Stireman, 2003) and sex ratio (van Nouhuys and Laine, 2008). Although a host species may kill many of its endoparasitoids, in rare cases both parasitoid and host survive to maturity (Section **10.2.5.7**), probably to mutual detriment.

11.4.4.2 Temporal and spatial density dependence in empirical data

From Howard and Fiske's time the concept of density-dependent mortality has been a central issue in insect dynamics and continues to be so today (Dempster and McLean, 1998; Turchin, 2003; Section **10.2.3.9**). Density-dependent mortality can be investigated empirically in both time and space (Richards, 1961; Hassell, 1968; Walde and Murdoch, 1988; McClure, 1991; Hails and Crawley, 1992; Rothery, 1998), by plotting per cent mortality on population density (Freeman and Parnell, 1973; Royama, 1977). But as we saw (Section **10.2.3.7**) density dependence is not always direct, it is often inverse (Hails and Crawley, 1992).

Forrest's maxim (Section **10.2.5.1**) is applicable to a focal species as well as to its enemies. If it rapidly develops great numbers it often outstrips their depredations, the more so the greater its density, progressively producing inverse density dependence. In all there are three situations in which this effect occurs: (i) out-reproducing enemies, as in some psyllid bugs and aphids; (ii) emerging together in great numbers, like *Tipula paludosa*, (Section **3.2.1.2(f)**), some mayflies (Corbet, 1964) and several cicadas; and (iii) *en masse* immigration, as in locusts, *Choristoneura* and *Heliothis*. As Taylor (1984) remarked, 'movement confounds density and distribution', but it may also modulate density dependence. Any of these effects can put a species on the far side of Southwood and Comins' *natural enemy ravine* (see Fig. 11.11).

Apart from mortality, individual growth rates and fertility (Hanski, 1990; Section **10.2.2.4**) are other attributes affected by density. This is implicit in Verhulst's logistic. They compound to give r_m, the positive or negative growth rate of a population (Section **11.5.2.1**). Emigration rates may also depend on density (Nicholson 1933, 1959; Enfjall and Leimar, 2005; Section **11.2.2.2**). In models, density dependence is generally defined in relation to r_m (q.v.; Section **11.5**). Hassell (1998b), following Nicholson, has argued for its overriding action in population regulation. But density dependence in evolution was examined much later than in ecology, with MacArthur and Wilson's (1967) concept of r and K selection (Pianka, 1972; Mueller, 1997).

Pollard *et al.* (1987) endorse Huffaker and Messenger's (1964) view that density dependence occurs due to repressive ecological factors that, jointly or singly, intensify as density increases and relax as it falls. If the strength of a factor, identified by estimates, is, in turn, affected by the density of the organism on which it acts, it is density dependent (Royama, 1992). Or broadly, density dependence occurs when the per-capita growth rate of a population depends on its own density (Rothery, 1998). So for migratory species, density may affect the rates of decrease (mortality and emigration) and of increase (births and immigration). These broad definitions, however, tend to mask critical differences between intra- and interspecific processes and other effects from enemies, which as we saw include not only mortality but also reduced AF and often dispersal (Section **10.2.3.8**). Naturally, these rates relate to density of a population under study in its local habitat. The density status of *immigration rates* is rarely considered. But if *regional* densities are high, as in outbreaks, there may be great numbers of aerial migrants (Taylor, 1986). So these rates too will be density dependent on extensive spatial scales, and may well have stabilizing effects on local populations.

When the effect of a given factor, say percentage death from an enemy, is plotted on density in a given place (often a single patch) over several successive generations, *temporal density dependence* may be revealed. This is best analysed by regression. The parameter β, estimated by the statistic b derived from the data, defines the slope of the line. Higher values of b describe steeper slopes. But a factor causing density-dependent mortality may be reactive to increasing density (b is high) or shows little increase with respect to density (b is low). Clearly, within the patch, factors producing higher values of b will be able to restrain population growth better, although both are statistically density dependent. In fact, when β is in unity there is perfect regulation (Varley and Gradwell, 1970), while values >1 may lead to widely fluctuating numbers. So: *the significance level of the slope is different from its regulatory power.* Such mortality may be statistically significant but insufficiently strong to restrain numbers (Hanski, 1990). When the intercept (a) of the graph is negative the regression line cuts the x-axis some distance from the origin, namely death from a factor occurs only above a threshold value (see Fig. 1 in Kowalski, 1977). This also may occur when mortality results from competition. Unfortunately, density dependence often becomes confused with population regulation, which is clearly in error.

For spatial density-dependent mortality, we can (i) compare the same spatial level (e.g. within food items, or patches, or habitats; Section **12.2**) in a single generation. Such a factor could be investigated between different patches, say ten trees inhabited by a defoliating caterpillar, in the same generation. (ii) One can see how such a factor varies at different spatial levels, an approach combining space and time (Heads and Lawton, 1983; Freeman and Smith, 1990). Temporal density dependence at several spatial levels may be assessed giving a spatio-temporal matrix of information. Such an effect may occur at one spatial level, say the patch, but not at another, say the habitat. This often relates to the scale of movement (Dempster and McLean, 1998) and/or the scale of the enemy's perception (Hails and Crawley, 1992). (iii) Spatial density dependence from retrospective data, with time suppressed, can be investigated in several habitats inhabited by a species (Freeman, 1973a, 1977; Freeman and Parnell, 1973; Fig. 11.17). Thus, in *Sceliphron,* density-dependent parasitism from *Melittobia* occurs from patch to patch. At 34 sites in southern Jamaica, those with denser breeding populations suffered greater mortality ($P < 0.001$). But the causes are complex, since secondary wasps nesting in old *Sceliphron* cells are also *Melittobia's* victims. This enemy maintains its local numbers in the absence of the primary host (see Fig. 10.16). There is trans-specific parasitism.

Further types of such mortality exist. Temporal density dependence may have a time delay (Varley, 1947), as in the winter moth (Varley *et al.*, 1973; MacPhee *et al.*, 1988; Fig. 11.18). The concept has importance in deductive models involving enemies (Turchin, 1990; Section **11.5.2.3**). In spatial density dependence independent of time, any delayed effects are included in the result, but cannot be isolated. Pollard *et al.* (1987) review tests of density dependence in census data, including the well-known one by Bulmer (1975), finding several faults. These result from unrepresentative, inadequate and/or inaccurate field data, often due to a failure to measure emigration and the numbers *entering* each stage (Section **11.4.2**). So, over the last several years efforts have been made to improve them. Pollard *et al.*'s method and that of Berryman and Turchin (2001; Section **11.3**) for identifying

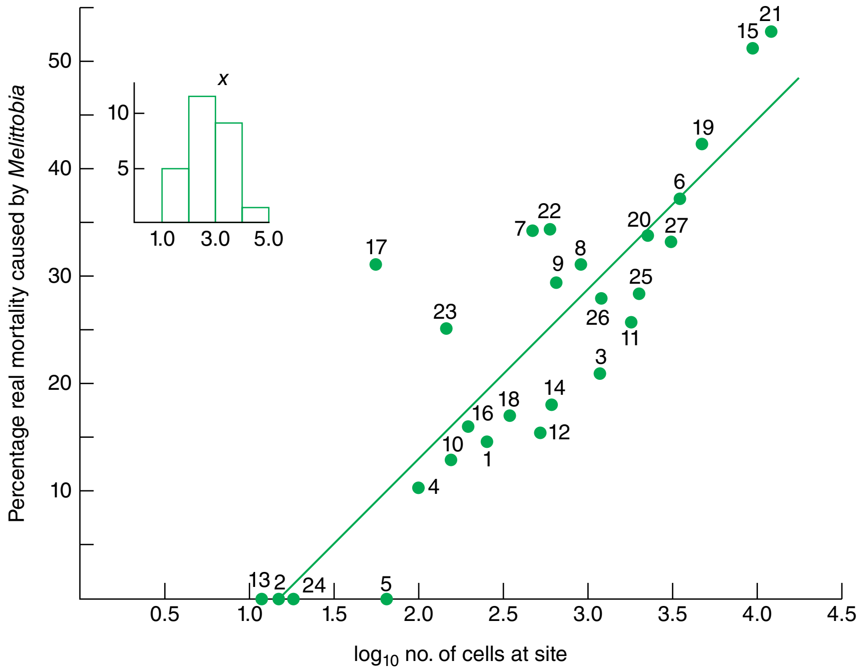


Fig. 11.17. Spatial density-dependence on a global scale. Data from: Freeman, B.E. and Parnell, J.R. (1973) Mortality of *Sceliphron assimile* Dahlbom (Sphecidae) caused by the eulophid *Melittobia chalybii* Ashmead. *Journal of Animal Ecology* 42, 779–784. Fig. 2a, p. 782. Reproduced with permission.

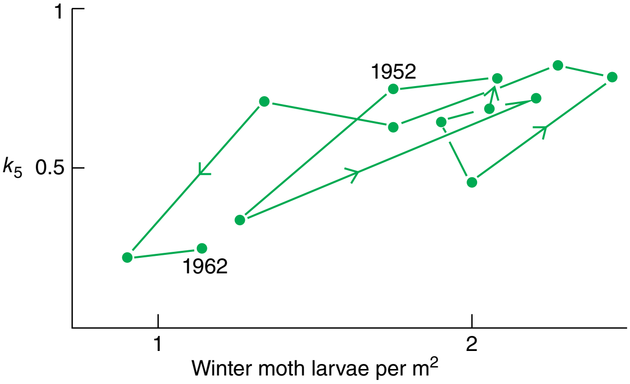


Fig. 11.18. Delayed density-dependence in the winter moth. From: Varley, G.C., Gradwell, G.R. *et al*. (1973) *Insect Population Ecology*: *an Analytical Approach*. Oxford: Blackwell. Fig. 7.6. Reproduced with permission.

density dependence in time-series data give much improved results.

11.4.4.3 Metapopulations and cyclic budgets

Although Andrewartha and Birch (1954), following Thompson and Nicholson, developed the fragmented population concept, Levins (1970) coined the term 'metapopulation'. There are two types: (i) there exists a large, permanent 'mainland population', the source of migrants to several, smaller 'island populations' between which migration is effectively absent (*mainland-island model*); and (ii) there exist patchy habitats of different sizes between which migration occurs (*Levins' model*). Compare these concepts to those in Fig. 12.4. These models have been applied to assemblies of species. One should also separate the effects of population size

(= number) from that of habitat area. See Harrison (1991), Hastings (1996) and Section **12.1**.

Morris (1963) and associates (C.A. Miller, D.O. Greenbank, D.G. Mott, K.E.F. Watt, *et al.*) studied the outbreak of *Choristoneura* (Section **5.2.1.4(c)**) in the late 1940s and 1950s in New Brunswick, Canada. The moth inhabits extensive stands of balsam fir, a metapopulation covering ~35,000 km^2. Their work is one of the most detailed studies of an insect population. During 1948–1957 they constructed some 80 life tables, but they give only a 'typical' table (see Table 2.1; see Section **11.4.1**), not a combination to produce a retrospective one.

But retrospective tables (Freeman, 1976; Freeman and Mulder, unpublished data; Section **11.4.3**) are uniquely suited to study metapopulations such as that of *Choristoneura*. For *Sceliphron* in Jamaica, they show that low-density isolates on the edge of distribution have far lower juvenile mortality than dense ones in the centre (Freeman, 1977), namely wide-scale spatial density dependence (Freeman and Parnell, 1973). But, in a similar sphecid wasp, *Trypoxylon palliditarse* in Trinidad, the opposite is true (Freeman, 1981a; Section **12.1**): *inverse* spatial density dependence. Using such tables, mortality distribution across a metapopulation is revealed. Were they applied to examples, such as those in Section **10.2.5.1**, where AF is high and juvenile mortality low, they might well show loss during redistribution to be the major feature of mortality, as in *Melittobia* (Freeman and Ittyeipe, 1993). This may also be the case in *C. fumiferana*, since apart from great *larval* attrition during redistribution, 49% of adult females failed to lay eggs (Greenbank, in Morris, 1963). For *Conophthorus* beetles (Section **6.3.1.1(c)**), however, periodic shortages of cones, namely great reductions in the habitat's carrying capacity (Dempster and Pollard, 1981), would be a major feature of its dynamics.

General cyclic budgets quantify major aspects of LHS: AF, juvenile mortality, sex ratio and losses during redistribution and resource finding (Section **11.4.3**). But being independent of time they omit the duration of the life cycle. While local budgets reveal spatial effects, general budgets cannot refer to spatially dependent and time-dependent features of LHS, as both space and time are collapsed. But we also see that of Andrewartha and Birch's three questions, only question two is completely time-dependent.

11.5 Mathematical Models of Population Processes

11.5.1 General introduction

Mathematics employs different reasoning from that used in empirical science, *deduction* as opposed to *induction*. Starting with the Pythagoreans ~530 BC and continuing in Plato's Phaedo, deductive reasoning was promoted as the only certain and so *highest* form of knowledge. Unlike inductive knowledge, which arose from personal perception and was flawed by the limitations of our senses ('sight and hearing are inaccurate witnesses'), it is held to provide universal truths (Russell, 1961). While deductive reasoning is certain and inductive reasoning can attain only 'a very high degree of probability' (Thompson, 1956), it is one of the most pernicious doctrines ever perpetrated, belittling observation and experiment, permitting the rule of dogma and has possibly strangled the development of western art and science by a millennium.

The difference between induction and deduction is explained simply in Robert Persig's unique novel (1974) *Zen and the Art of Motorcycle Maintenance*: 'That is induction: reasoning from particular experiences to general truths. Deductive inferences do the reverse. They start with general knowledge and predict a specific observation. That is deduction.' The SOED definitions are: 'Deduction: Inference by reasoning from generals to particulars. Induction: The process of inferring a general law or principle from the observation of particular instances'. Mentis (1988) schematizes the relationship between induction and deduction. So, the true nature of biological science is inductive, *deduction is ancillary* (Thompson, 1956).

We will not venture too far into the field of demographic, mathematical models, emphasizing empirical data as is appropriate in a book concerned with the autecology and control of pest insects. But today mathematicians and biologists often collaborate to study population dynamics, a blend of deduction and induction to mutual benefit if an increasing fund of data allows better models to be framed. It is not so if it is thought that ecological problems can be solved far from the field (Taylor, 1984). While mathematicians forage in biological fields for new relationships and value conceptual elegance (Waage, 1986), biologists want mathematics to unravel natural systems and may struggle to understand what their partners are saying (Levin, 1980). Fisher (1930) notes 'The types of mind which result from training in mathematics and in biology certainly differ profoundly …', adding that despite biology's observable complexity, the mind mathematical is less constrained than the mind biological. Biologists look, say, at sexual versus asexual reproduction, mathematicians could investigate outcomes of there being 1, 2, 3, … *n* sexes! Happily, the link is two-way: biology brings to mathematics as much as mathematics brings to biology (Murray, 1989).

Population mathematics is a vast field, concerning not only ecology but also human demography and epidemiology. Here I introduce readers to 'this burgeoning body of literature and the points of contact it makes with the real world' (Hassell, 1980). But models condition our perception (Wiens, 1976; Pielou, 1981; Margolis, 1993). So in defining competition (Section **9.8**), we must avoid importing the findings of models, since these may cloud rather than clarify perception, especially when natural heterogeneity is ignored (Walter, 1988b; Remmel *et al*., 2009). Even so, Gavrilets (1999) suggests silkily that models may 'train our intuition about complex phenomena', and Hanson (1961, in Rieppel, 2004) argues against 'theory-free' observation. This is hardly material since any ecologist observing has been exposed to theory anyway.

But field biologists have long regarded models with suspicion. Varley (1941) remarked: 'A mathematical theory is a description of the relationships between things in nature, which, for the sake of convenience is greatly simplified'. Huxley (1942) notes that 'deduction and mathematical generalisation can only achieve valuable results with the aid of a firm foundation of fact'. Sheppard (1956) says 'This mathematical approach tells us what will happen … under the conditions laid down by the model, but it does not show us whether the model, in fact, represents the situation found in nature'. Field investigations must precede detailed modelling, as in work by Dwyer *et al*. (2000) and Turelli *et al*. (2001). For ecology, a model is valueless unless it illuminates the natural world to the ecologist. Pielou (1981), herself a notable statistician, complains: 'Models are being constructed, refined, elaborated, tinkered with and displayed with little or no effort to link them with the real world'. This is 'armchair ecology'. Trying to understand the real world because we can predict the behaviour of simple laboratory systems misses the point (Schaffer, 1985). My view (Section **10.1**) is that empirical autecology should *seek to reveal* natural complexity (see Hansson, 2003). It is against such complexity that models can best *seek the essence* of real population processes, not omit awkward facts for the sake of mathematical tractability. Macaulay noted in his History of England (1848) 'never remove an anomaly simply because it is an anomaly'. Further, in ecology mathematics is a servant not the master. Again, the deductive method 'must not be allowed too free a rein' (Huxley, 1942).

Mathematical models in biology, or for that matter in any other field, start with axioms concerning the study system that arise from our limited knowledge of it. But just as it is hard to know if one has framed all possible hypotheses in *induction*, so the illustrious mathematician David Hilbert pointed out that it is hard to know if one has included all the necessary axioms in *deduction*. Then Gödel's incompleteness theorem 1932 (Nagel and Newman, 2008) shows that with integers, no finite set of axioms will suffice to prove the truth of all correct arithmetical statements. Moreover, the set of axioms themselves cannot be used to prove that they are free of internal contradiction. So, even within mathematics there is potential inconsistency.

Pielou (1981) says that:

> Modelling consists in constructing, mentally, a plausible symbolic representation of the functioning of an ecosystem [she means *any* ecological system], in the form of mathematical equations. One then tests whether the behavior of the ecosystem conforms with that of the model.

But in models some axioms are for simplicity knowingly omitted. Thus, Verhulst's logistic (Section **11.1.2**) omits the axiom of a place in which the supply of consumables varies in time, both are subsumed in a constant *K*, the carrying capacity, that is, the maximum number of animals the place can support. There are no time lags and all individuals are identical. There are no instars or variation within them. The latter means that this and many other models are based on population, not on individual, attributes (Łomniki, 1978; Leather and Awmack, 1998). But individuals are the basis of autecology and evolution. This assumption also runs roughshod over risk spreading (Section **9.7**). When models lead to false predictions, however, the axioms are inadequate or misplaced, not that the mathematics is wrong. But models with more state variables may not be any better, because the parameters are estimates, never known precisely (Pielou, 1981; Turchin, 2003). Detailed predictions need detailed knowledge and may be contingent on the circumstances (Lawton, 1999). In about 1690, John Locke noted that we should 'not entertain any proposition with greater assurance than the proofs it is built upon will warrant' (Russell, 1961). So, conclusions contain *only* what is in the axioms (Harcourt, 1969; Maynard Smith, 1983b). *Postulates* are probable processes, lacking the innate verity of *axioms* (Turchin, 2001). For field ecologists the truth of the axioms allows assessment of the truth of the model, but they must accede to the validity of the mathematical operations. So another sequence exists:

Biological axioms (or postulates) →
Mathematical operations →
Biological conclusions

With all their limitations, the merit of models from the empiricist's viewpoint is that they force economy of thought. 'They are more powerfully used as a starting point to organize and guide understanding' (Holling, 1973). They also bring fresh ideas to biology, such as the models by Dusenbery (1989; Section **10.2.4.5**) of the behaviour of searching insects flying in moving air. Models should facilitate insight by 'abstracting and incorporating just enough detail to produce observed patterns' (Levin, 1992). Stamp (2003a) regards them as a key element in the refinement and maturation of theory: one sees what happens in that subset of reality defined by the model. The result may be counter-intuitive (Murray, 2000) and/or reveal insights that help empirical investigation (Gilpin, 1973). Southwood (1977) feels that progress in dynamics, following Huxley (1942) for evolutionary theory, needs a combined 'assault' from induction and deduction.

Empirical science, then, starts with gathering and organizing data. Although there had been inputs by Roger Bacon (1214–1294) and during the Renaissance (Kline, 1972), its development began in the main with Francis Bacon (Platt, 1964), a chimerical man of suspect morals but innovative insights, mooted author of 'Shakespearean' plays. From this empirical base, the '*Great Instauration*', classifications could be developed and hypotheses framed and tested, or more stringently, falsified. As Bacon noted, 'negative instances must be sought'. David Hume (1711–1776) proposed that knowledge increases by the perception of error rather than that of truth, an attitude promoted by Platt, and developed by the Vienna School of philosophers, of whom in science Karl Popper (1989) is the best known. Even so, 'the search for confirmatory evidence is easier than the search for falsification and is very seductive' (Simberloff, 1981; Turchin, 2003, p. 8). Thus, observation and hypothesis should go hand in hand (Platt, 1964; Carr, 1987), sometimes to the former's detriment for the same phenomena may be seen differently when guided by different theoretical frameworks (White, 2001; Walter, 2003). But social, political and national attitudes can bias our judgement too, to which Bacon drew attention as 'idols [errors] of the theatre', while Russell (1961, Chap. 12) inquires 'What has been the influence of … social circumstances upon the thoughts of … original thinkers …?' W.D. Hamilton (1996) was the butt of this subjectivity when a postgraduate at London School of Economics.

But the number of possible hypotheses is unknown. Hence, effort and ire may be expended trying to 'prove' one or other of two conflicting ideas, when neither is true, when both are special cases of the same phenomenon, often relating to two ends of a spectrum. Co-operation may be more fruitful than contention, a Buddhist imperative, as in the work by Abrams and Ginzburg (2000) (Turchin, 2003). Chamberlin (1897) warned that precipitate explanations have a way of becoming accepted prematurely and so influence further inquiry, ones that Watt (2000) termed 'paradigm-based limits to knowledge' (see Jermy, 1984). Such an attitude is closer to the Devil Dogma than to science. Following Chamberlin, to avoid such pitfalls one should produce multiple hypotheses (Scheerer, 1963; Platt, 1964), which it may be possible to refine or synthesize. Critically, Popper explains that hypotheses are at two levels: (i) *conjectures* – as to what *might* be going on; and (ii) their rigorous testing, potentially *refutations*.

Conjectures are valuable as they may embrace an original idea that can be refined and tested later. Assembling a large database is a wise beginning (Simberloff, 1981), then better-informed hypotheses can be framed. I think that testing deductive models based on simplistic axioms is to do ecology the wrong way round. Good field observations are the starting point (Applegate, 1999). But it may become increasingly hard to separate hypotheses, even to limit them! A hypothesis may be, say, only 80% correct. Should it be rejected? No: we accept it until a better one is made (Simberloff, 1981; Turchin, 2003; Stephens *et al.*, 2006). *Hypotheses are essentially iterative* anyway. Like rationale applies to *classifications* that are substantially, not totally, comprehensive (Gauld, in Waage and

Greathead, 1986). The World Biological is indeed a can of worms, but following F.E. Smith, the barrister not the biologist, while we may be none the wiser we will be better informed! The good news for field ecologists is that hard empirical data stand firm in perpetuity. Representativeness and accuracy are key. Later such information may be used in meta-analyses, and interpreted in new ways, as in Hunter's (1998) re-analysis of Varley and Gradwell's data on winter moths. Models do not become invalid by reason of age. But better ones should supersede them, 'better' meaning simpler, more tractable, and/or those that reflect nature more accurately.

Some workers have engaged in what has been memorably dubbed '*physics envy*', wishing ecology had the precise laws of that discipline (Cohen, 1971; Lawton, 1999; Murray, 2000). But the laws of physics are neither perfect nor without exception, auxiliary hypotheses often being necessary to accommodate wayward data (Turchin, 2001; Colyvan and Ginzburg, 2003). Witness Einstein's vain search for a unified field theory. In astrophysics, we wait for predictions to occur: we cannot manipulate the Universe! While the laws of fluid dynamics that govern the weather are known, its vagaries cannot be predicted for more than a few days (Section **2.2.2**). Murray (2000) proposes several firm laws in ecology and evolution. Turchin explains that some laws in population dynamics, such as exponential growth and consumer-resource oscillations, are well substantiated. Even so, and like weather patterns, they are overlain by environmental noise; maybe by chaotic components. Importantly, we must embrace variation of ecological data, rather than attempt to reduce it to simple models, since it embodies more information (Hansson, 2003).

Mathematical modelling in population genetics started in 1908 (the Hardy–Weinberg equilibrium) and was advanced by 1930 with R.A. Fisher's *The Genetical Theory of Natural Selection*, and Haldane's (1922, 1932) and Wright's (1931) classic works. More models were developed with the work of Lotka (1920, 1925), Thompson (1922, 1924) and Volterra (1926). A later surge in their growth took place with the development of computers. Gillman and Hails (1997) give a detailed review, while Turchin (2003) considers time-dependent dynamics, making the concepts intelligible to lightly mathematical readers. Being a field ecologist, I have relied on this important book to compile much of Section **11.5.2.**

The axioms of the deductive approach to dynamics give us an idea of its difference from the empirical one. Thus: (i) population growth is innately exponential; (ii) there exists an upper density bound (ceiling) bringing about population self-limitation; (iii) the number of resource items found by an individual consumer is proportional to their density when this is low; (iv) the amount of energy an individual can obtain from its victim is some function of the latter's biomass; and (v) no matter how high the density of a food resource may be, there exists an upper physiological limit to the rate at which an animal can process it. These axioms come from basic biology, not detailed research. Density dependence is defined differently, as 'Some (nonconstant) functional relationship between the per-capita rate of population change and population density, perhaps involving [time] lags' (Turchin, 2003). Hanski *et al.* (1996) in a metapopulation model where local populations obey a random walk, define it as the 'frequency of hitting the ceiling per generation per population'. These definitions usually refer to bounded populations lacking immigration although redistribution occurs within them. Nor do they recognize evolution (Section **11.2.3**). So, differences exist between a model and a real system, the latter being influenced by many external factors not in the model (Holt and Lawton, 1994). Turchin (2003, p. 58) writes:

> real-world populations ... are affected by a multitude of different factors, some of which we model explicitly while others we have no choice but to leave out of the model. Nevertheless, these exogenous factors – fluctuations in weather, immigration events, erratic fluctuations in food resources or natural enemies, and so on – continuously affect population change.

I refer to such cases below and show how the demographic approach over-simplifies real systems (Pielou, 1981), or as May (1973) puts it harshly, produces 'caricatures of reality'.

A further difference of mathematical models from the results of empirical studies is that they often centre on analyses of simple time-series estimates of population numbers (Section **11.3**). Life tables (Section **11.4**) add much greater demographic detail, as ideally, they attempt to estimate the fate of every egg laid in a population (Section **12.2**), usually sampled in a series of generations. While such data may be used in models to estimate parameters such as rates of predation and parasitism, they may be handled more representatively by matrix analysis (Caswell, 2000). Indeed, this method is useful for insect data for each of several instars (Turchin, 2003). Oscillations in time series are numerical fluctuations having an element of regularity, thus allowing some degree of prediction. First-order oscillations arise from systems having feedbacks with time lags of a generation or less. Typically, they have a period of two to four generations. Second-order oscillations have feedbacks with time lags more than one generation and have a periodicity of approximately 6 to 12 generations (Turchin, 2003). Those within this band of frequency are common in the dynamics of forest moths (Myers, 1998).

We have space to sample some population models, both classical and recent. With continuous dynamics, *differential equations* are appropriate; with discrete dynamics, often annual generations, *difference equations* are better (Pielou. 1981). First, *time-dependent models lacking spatial co-ordinates* (aspatial) come as follows: (i) single species: population growth (Section **11.5.2.1**); and (ii) two species interactions: interspecific competition (Section **11.5.2.2(a)**) and predation and parasitism (Section **11.5.2.2(b)**). But they are only half the story. Second, we examine models in which a population inhabits several locations (Sections **11.5.3** and **12.1**), *recognizing spatial effects and/or metapopulations*, a big step towards realism. Throughout, I will comment from a field ecologist's viewpoint on the appropriateness of these models to the real world of autecology.

11.5.2 Time-series models: Aspatial effects

11.5.2.1 Single species: Population growth (including intraspecific competition)

There are four common measures of population growth. First, the intrinsic rate of increase *r* (best denoted by r_{m} where possible to avoid confusion with the correlation coefficient, and termed the 'innate capacity for increase', the 'm' referring to Malthus, who emphasized the exponential nature of population increase) (Leslie and Ranson, 1940; Gaston, 1988). It is estimated and hence a *statistic* (Section **11.4.1**) and combines fertility and mortality in a single value. Second, the net reproductive rate r_o is the ratio of total female births in two successive generations, namely the per-capita rate of population change (Turchin, 2003). Third, the finite rate of increase $\lambda = e^r$, is the number of births/female/week (Andrewartha and Birch, 1954). Finally, Laughlin (1965) proposed the statistic r_e, which is close to r_m, but gives the actual rate of increase of a population with discrete generations and that of one breeding continuously under certain conditions. Other measures are *G*, the generation length, and *DT*, the doubling time (Eliopoulos, 2006; Chmielewski *et al*., 2010).

For $r_m = 0$, population numbers are constant, positive values quantify an increase and negative ones a decrease of population at various rates. With overlapping generations and continuous breeding, as in stored-products pests in warm environments (Section **6.3.1.2**), differential equations are normally used. If the rate of reproduction is held to be a constant, population increase is defined by:

$$dN/dt = B - D = bN - dN = (b - d)N = r_oN \tag{Eq. 11.1}$$

where *N* and *t* are as before, *B* and *D* are the total rates of births and deaths, *b* and *d* the per-capita rates, r_o is the per-capita rate of population change. There are no migration terms since the population is defined as closed. The logistic equation of Verhulst, which we met in Section **11.1.2**, is a natural generalization:

$$dN / dt = \gamma_o N(1 - N / K) \tag{Eq. 11.2}$$

on the assumption that there is a fixed carrying capacity, *K*, that limits population growth absolutely.

To repeat, population dynamics are inherently non-linear (Turchin, 1999). But even within the restraints of an aspatial population (Walter, 2003) the logistic suffers from other well-known deficiencies: (i) r_o is related linearly to *N*; (ii) no time lags exist; (iii) the population has no age structure; and (iv) exogenous factors (Section **10.1.1**) have no influence. An improved model in which population growth peaks at some intermediate density and so shows an Allee effect (Section **10.2.2.4**) employs a polynomial quadratic (Turchin, 1993, p. 331):

$$dN/dt = b(N - a)(K - N) / K^2 \tag{Eq. 11.3}$$

where *a* is the density below which population growth is negative, and *b* a constant related to how fast the population will grow maximally. Weibull distributions are a family of asymmetrical curves (Pinder *et al*., 1978; Pielou, 1981) that have some advantages in describing growth or survival data, be they for plant or insect populations. Southwood and Comins (1976), in their synoptic population model, also incorporate an Allee effect in the reproductive rate by the following:

$$\mathrm{Rep}_t = \lambda[1 - \exp(-N_t/f)]\exp(-N_t/q) \tag{Eq. 11.4}$$

where λ is the finite net rate of increase, incorporating fertility and, for the purposes of their model, density-independent mortality. Then, f and q are parameters reflecting respectively positive effects (co-operation) and negative effects (intraspecific competition and perhaps cannibalism) of population density.

Intermediate population situations occur quite often, as in many forest moths and pest beetles. During the period of reproduction, say May–September, both the birth rate b and the death rate d will be positive, so that excluding redistribution, numbers are determined by their relative magnitudes. But during the harsh season there is no reproduction ($b = 0$) while d remains positive, and hence numbers decline. Turchin (2003, Eq. 3.14) models this more realistic situation within the logistic framework as follows:

$$dN/dt = r_{avg}[1 - e\Sigma(t)]N - (r_{avg}/K)N^2 \quad (\textbf{define } e) \qquad \text{(Eq. 11.5)}$$

where $\Sigma(t)$ is some annual function that varies from −1 to +1, r_{avg} is the intrinsic rate of population increase averaged over all seasonal values and K is the carrying capacity averaged in the same way. If $e > r_{avg}$, then both the intrinsic rate of increase and the carrying capacity will be negative during the harsh season. But, of course, field capacities have a minimum value of zero. Even so, the situation characterizes many insect species in temperate regions, where reproduction during winter is impossible. **Equation 11.5** also relates to 'harsh' and 'kind' environments (Section **11.2.2.3**) of Andrewartha and Birch's theory, and accounts for the fact that the K of real environments is variable in space and time (Gilpin, 1973; Enright, 1976; Dempster and Pollard, 1981; Turchin, 2003). Pine cone beetles (Section **6.3.1.1**), *Asphondylia* midges (Section **12.3.4.3**) and mosquitoes breeding in temporary pools provide good examples. For grazing mammals in East Africa, seasonal rainfall promotes plant growth and hence a greatly increased regional carrying capacity, which these beasts track in their seasonal migrations. In Section **12.2.1** we will relate K to the levels of environmental space.

With discrete, generally annual generations, we employ difference equations. The *realized per-capita rate of population change* r_t is then:

$$r_t = \ln(N_t/N_{t-1}) = \ln N_t - \ln N_{t-1} \qquad \text{(Eq. 11.6)}$$

where $\ln N_t$ is the natural logarithm of population density at time t (Turchin, 1999).

Two derivatives of the logistic in the discrete form (Turchin, 2003, pp. 52–55) are Ricker's model:

$$N_{t+1} = N_t \exp[r(1 - N_t/K)] \qquad \text{(Eq. 11.7)}$$

and Beverton and Holt's model:

$$N_{t+1} = \lambda N_t/(1 + (\lambda - 1)N_t/K) \qquad \text{(Eq. 11.8)}$$

As before, $\lambda = e^r$. It is generally assumed that if fecundity is high, juvenile mortality will also be high (Price, P.W., 1997; Sections **10.2.5.1** and **11.4.3**). But this is not always so, as in the fruit fly *Dacus oleae*, *Conophthorus* beetles, the parasitoids *Eupelmus* and *Melittobia*, and sparse populations of *Asphondylia* (Freeman and Geoghagen, 1989). It is also typical of several parthenogenetic aphid populations and may be far more common than generally realized, an example of Chamberlin's (1897) 'precipitate explanations' (Section **11.5.1**). Naturally, such a situation leads to rapid increases in numbers, as in pest outbreaks, which are of special interest to us. Because these population models are bounded, namely confined to a fixed area, numbers and population density are equivalent (Section **9.3**) and interchangeable. There is no number/density anomoly. Also, they are *deterministic*: given a set of starting conditions there can be only one outcome. But biological systems are unlike this, since chance is always a player (Mandelbrot, 1977; Benton *et al*., 2006). Equations incorporating chance, called *stochastic* equations, were developed for population growth. One can do this by varying the parameters, such as the carrying capacity, randomly (Turchin, 2003).

A further feature of some model equations, both continuous and discrete, is that they may be chaotic. This is unwelcome if we use such models to forecast pest outbreaks, although Vandermeer (1982) suggested that chaotic populations would be sparse. By using deterministic equations, we have come to assume that real populations are at equilibrium (Hastings *et al*., 1993), another precipitate explanation! In contrast to chaotic dynamics, exact values of initial conditions are trivial in equilibrium dynamics.

11.5.2.2 Two species: Interspecific competition (Sections 9.8 and 10.2.3.10)

In the equations in Section **11.5.2.1** inimical effects of other species are included in the death rate, d, or subsumed in the carrying capacity. Here they are modelled explicitly. The interactions fall into two distinct categories: *interspecific competition for a scarce resource* (food or space within the habitat; Section **9.8**), and *predation, including attack by parasitoids* (Section **11.2.5.3**). Both have continuous and discrete versions. The former, the Lotka–Volterra equations derived independently by Lotka (1925) and Volterra (1926), are based on Verhulst's logistic, a continuous form of which is given for each species:

$$dN_1/dt = r_1N_1\left(1 - N_1/K_1\right)$$

$$dN_2/dt = r_2N_2\left(1 - N_2/K_2\right) \qquad \text{(Eq. 11.9)}$$

The terms are as in **Eq. 11.6**, the suffixes 1 and 2 refer to these two species. As Verhulst's equation refers to a closed system, it is assumed that the two interacting species share a fixed space. So far little has been added to Verhulst, but a term modelling the interaction strength between the two species can be appended:

$$-\alpha N_1N_2 \qquad \text{(Eq. 11.10)}$$

where α is the factor expressing this inequality and the idea that the quantity but not the identity of the resource that each species requires within their shared living space is different. Note that the requirements of individuals in species two are in units based on those of species one. This leads to two equations:

$$dN_1/dt = r_1N_1\left(1 - N_1/K_1 - \alpha N_2\right)$$

$$dN_2/dt = r_2N_2\left(1 - N_2/K_2 - \alpha N_1\right) \qquad \text{(Eq. 11.11)}$$

The possible outcomes are: (i) species 1 eliminates species 2 or vice versa; or (ii) there is co-existence. For elimination we expect the inimical effects of one species on the other to be greater than any return effect, namely competition is asymmetrical. With co-existence we expect such return effects to be insignificant. This rationale leads to a broad definition of interspecific competition in which 'two species compete when an increase in the density of one species leads to a decrease in the density of the other, and vice versa' (Tilman, 1987; Section **9.8**). Combining diverse processes in a single term in so complex a subject it invites confusion (Walter, 1988b) and so is not adopted here, except of course in equations embracing the concept.

The first outcome has been discussed intensely for field situations under the title *the competitive exclusion principle* (Cole, 1960; Hardin, 1960; van Valen, 1960; Patten, 1961), although *competitive displacement* is better (de Bach, 1966). Probably such real-world interactions operate only at high population densities and at isolated parts of the joint distribution (Pielou, 1981; Connell, 1983; Walter, 1988b). Indeed, the outcomes of such competition, even in models, are complex and variable (Slatkin, 1974; Hanski, 1983). Highly mobile species like aphids and mosquitoes should suffer only patchy competition (Levins and Culver, 1971). Recall that *individuals compete*, and populations compete as a consequence. The form of the species-abundance distribution (SAD) (Williams, 1964; Hughes, 1986; Williamson and Gaston, 2005; Section **9.4**) shows that low densities are the rule and high ones the exception. In Milne's theory (Section **11.2.2.4**) imperfect density dependence is held to be largely responsible for this situation in nature. The dynamics of the two populations are not inextricably linked, as the interactive term $-\alpha N_1N_2$ assumes. They have 'decoupled' dynamics, as Thompson (1929) pointed out. Some models (Armstrong and MacGehee, 1980) predict that, due to an internally generated cyclicity, *n* competitors can persist on $k < n$ resources. For them competitive exclusion 'applies in general only to co-existence at fixed densities', which sounds artificial. In nature, a weaker competitor in terms of survival can compensate by higher AF (Pielou, 1981) or by being a good colonizer (Skellam, 1951; Hanski, 1983). Because of natural spatial complexity, competitive exclusion is unlikely in many insects (Wellings, 1987), agreeing with earlier models (Levins and Culver, 1971; Slatkin, 1974; Shorrocks *et al.*, 1984; Section **11.5.3**).

In metapopulation models of dynamics, local and regional time scales can be critical (Hanski, 1983). Divergence between these scales facilitates co-existence. Aggregation is important too, when it increases 'it becomes harder for the superior species to exclude the other' (Shorrocks *et al.*, 1984). In model self-organizing dynamics, persistent high-density islands of competing species persist in a given habitat (Hassell *et al.*, 1994). As in parasitism, predation can influence the outcome of competition (Slatkin, 1974; Caswell, 1978). Reading Milne (1962) (Section **11.2.2.4**) and Strong (1986) this is unsurprising. Again, we expect genetic imperatives. Lande and Shannon's model (1996) shows that genetic variability has diverse influences on population persistence, and a metapopulation study (Huxel and Hastings, 1998) reveals that the relationship between population size and extinction is critical, a result not found in some earlier models (Slatkin, 1974).

To return to the world of observation, Williams' (1947, 1951) re-analyses of David Lack's field data on birds, shows that *closely related species tend to be found living together*, despite Darwin's opinion (above) that the struggle for existence between them should be more intense than that between unrelated species (for an assessment, see Strong, 1980). Williams' conclusion also applies to *Dolichopeza* in the USA (Byers, 1961) and to crane flies in general in England (Freeman, 1968). A sophisticated analysis of 15 years of trap catches of syrphid flies at a single site (Gilbert and Owen, 1990), gives little evidence that competition structures their community. Indeed, related species, having diverged recently from a common ancestor, are expected to have many *similar* attributes (Byers, 1961; Freeman, 1968; Walter, 1988b; Björklund, 1997; T. Price 1997; but see Section **12.3.4.4**(e)) and so similar basic ecology. But *if* competition between them has had effects on fitness we expect natural selection to have reduced it. Fitness is relative (Fisher, 1930; Wall and Begon, 1985). If individuals of both species are affected equally there will be no fitness change. But there should be a *selective premium on the emergence of differences* between related species should they come together (Mayr, 1963) or remain together. This applies to all interactions reducing fitness. In models of such *ecological character displacement* (Slatkin, 1980), whether characters diverge or not depends on several assumptions, but especially on their relative value in two competing individuals, and that each species is limited by the same set of resources. Also, the relative density of the two species, ignored in many earlier studies, is critical. A further point is: 'what do we mean by living together?'. Species often occupy different patches within a given habitat (Section **12.2.4.2**) and/or different niches on a given plant. Again, recall from Section **9.10** that there is good emerging evidence for speciation in some such situations (Via, 2001).

While competition may not be operating now it might have done so in the past (Connell, 1980), causing niche separation, a possibility called '*the ghost of competition past*'. But Mayr (1963, above) had covered this idea. What is more, several, often related species, may live together. In Sweden, up to nine bark beetle species are found on single pine trees, but each has a separate 'niche' in either space or time (Trägårdh, 1927, in Elton and Miller, 1954). But no such niche separation exists in six *Erythroneura* spp. (Cicadellidae) living on American sycamore (Ross, 1958), nor in eight such species studied later (McClure, 1975). In a wide European survey, 22 insect species were found on roots and rosette meristems of three related *Centaurea* spp. (Muller *et al*., 1989). There are five feeding sites, but on the root collar, four *Apion* spp. all fed externally. Even so, <33% of plants were attacked, and <8% had more than one insect species! There was much unused resource. In Africa, the guild of scarabaeid beetles breeding in large mammalian dung has seven different ways of using it (Giller and Doube, 1989). But there is always the chance that something else may be driving niche separation (Walter, 1988b), such as ways to gather food more efficiently (Lovell, 1914; Section **8.2.1.1**).

In terms of real global dynamics, not models, a species survives in all places its members can find in which its *birth and immigration rates on the one hand, and death and emigration rates on the other have long-term balance*. If this balance occurs at high density it is common, if at low density it is rare (Section **9.4**). Recall two cases (Sections **9.8** and **10.2.2.5**) of potential competition. First, the fly *Pegohylemyia seneciella* avoids ragwort flower heads already occupied by the moth *Tyria jacobaeae* (Crawley and Pattrasudhi, 1988), but not vice versa. Second, two nymphalid butterflies *Inachis io* and *Aglais urticae* share the same stinging nettle food plant. But in neither case on a landscape scale do these insects consume more than a minuscule fraction of their food. Even if interspecific competition were a part of this balance it would not necessarily cause local extinction since its effects would likely fade away as densities diminish (Milne, 1962). But we can visualize a few *local situations* in which one species increases at the expense of the other, thus tipping this balance and driving the other's *local elimination*. Such competitive displacement occurs in two *Aphytis* parasitoids of red scale in California, ostensibly because the more successful one, *A. melinus*, is more vagile and uses smaller hosts, thus pre-empting their use by *A. lingnanensis* (Luck and Podoler, 1985). Walter (1988b), however, questions their conclusions. The interaction between *Pemphigus* and *Hayhurstia* (Section **9.8**) is a better example. Further cases of competitive displacement are given in Harcourt (1990), Kfir (1997) and Reitz and Trumble (2002). Competition and exclusion *could* happen and sometimes *do* happen, but will not *necessarily* happen. In other habitats there may be no competition but harsh physical conditions often tip the balance so that $b < d$ for both species, and continued existence is possible only because of continued immigration, that is, it is a *sink population* (Haldane, 1956; Freeman, 1981a; Hanski, 1998a; Section **9.4**).

To conclude, while several cases of *contemporary decline* of one species have occurred when another, often related species, moves in (de Bach, 1966; Denno *et al.*, 1995; Reitz and Trumble, 2002) we should be sure that competition, as in Section **9.8,** has caused it. Indeed, apart from direct enemy action, there are many non-competitive interspecific interactions (Andrewartha and Birch, 1954; Freeman and Parnell, 1973; Wootton, 1994; Jones *et al.*, 1997; Lill and Marquis, 2003). The inimical effects of shared enemies (*trans-specific mortality*) (Holt, 1977; Holt and Lawton, 1994; Juliano, 1998; Paine, in Reitz and Trumble, 2002), as shown in the field for solitary wasps (Freeman and Jayasingh 1975a; Freeman 1977, 1982; Section **10.2.3.9**), are probably more important (van Veen *et al.*, 2006). Such effects can operate throughout a great density range, and the suite of enemies is often extensive. Also, the decline of one species can be due to changes in the physical environment, and/or from anthropogenic causes (Reitz and Trumble, 2002; Walter, 2003), while possible genetic modifications coinciding with the appearance of a species should be borne in mind.

11.5.2.3 Two species: Predation models

These models include interactions of host insects and their parasitoids, which are a form of predation as far as the model is concerned since the host often dies (but not as often as formerly thought; Sections **8.2.2.1** and **10.1.2**). In those below, the predator or parasitoid is a *specialist* feeding only on one victim species. So their dynamics are necessarily coupled. These models were devised originally to explain the behaviour of laboratory microcosms (Pielou, 1981), for which they have been fairly successful. But complications arise in the field (Sections **8.2.2.1** and **8.2.2.5(j)**). Hassell (1978, 1998a, 2000), Jones *et al.* (1993), Gillman and Hails (1997), Abrams (2000), Turchin (2003) and Rockwood (2006) give general reviews. Early efforts date from Thompson (1922, 1924), Lotka (1925) and Nicholson and Bailey (1935). Berryman (1992) gives a fragmentary, historical review, omitting Thompson's seminal efforts to its detriment.

Thompson's (1922) discrete model assumes that parasitoids lay randomly in hosts without discriminating parasitized from unparasitized ones and so follows Poissonian statistics:

$$p(i) = \left(M^i / i!\right)\exp(-M) \qquad \text{(Eq. 11.12)}$$

where $p(i)$ is the proportion of hosts receiving i parasitoid eggs, and M is the mean number of eggs per host. As it is further assumed that all parasitized hosts die, surviving hosts have received zero eggs. Thompson also suggests parasitoid attack is effectively limited by egg supply, a feature that became known as *egg limitation* (Waage, 1986; Rosenheim, 1999a and b; Rosenheim *et al.*, 2008). The complete model is:

$$N_{t+1} = N_t \exp\left(-P_t F / N_t\right) R_0$$

$$P_{t+1} = N_t\left[1 - \exp\left(-P_t F / N_t\right)\right] q \qquad \text{(Eq. 11.13)}$$

where N is the host's population density, P the density of parasitoid females and F their mean AF. Thus PF is the density of parasitoid eggs, R_0 the host's reproductive rate, while q is the proportion of female parasitoids, which is frequently not 0.5 (Waage, 1986). No physical factors are modelled.

In nature enemies do not affect their victims in the same way (Section **10.1.2**). Predators disperse or kill their victims instantly. Parasitoid females lay eggs in or near their victims, but may also disperse them (Lima, 1998). Like predators they sometimes feed on and kill them, but also require nectar. Their larvae take a variable time to kill their hosts (idiobionts, koinobionts; Section **8.2.2.5**) but are often killed by them. The main caveats for **Eq. 11.13** (see Section **8.2.2.1**) and later models are:

1. Estimating AF accurately, since parasitoids, like many insects, often do not lay *all or any* of their eggs. This results from two linked causes: harsh weather and inability to find hosts.
2. AF is often influenced by food supply and if it is short, females may reabsorb eggs (Jervis and Kidd, 1986), although work by Casas *et al.* (2005) indicates this to be minor.
3. Synovigenic wasps often kill hosts by feeding on them (Flanders, 1947; Jervis and Kidd, 1991; Harvey *et al.*, 2015).
4. Parasitoids often discriminate against parasitized hosts.
5. There is a '*handling time*' (below).
6. Parasitoids may show *mutual interference*, so reducing their RS.

7. There may be *asynchronous interaction* (Varley, 1947; Hassell, 1969).
8. Some hosts may be in refuges.
9. Hosts and parasitoids moving between habitats and patches cannot interact (Weisser and Hassell, 1996), while parasitoids feeding and seeking cannot engage in parasitism. No similar effect occurs with predators, but see Section **8.2.2.4**(**e**).
10. Many hosts die from factors other than enemy action.
11. As above, predation has non-lethal effects, especially escape and dispersal.
12. Potential victims may deter or destroy their attackers (Salt, 1968).

With these caveats in mind, we can use the Lotka–Volterra model, doubled up from **Eq. 11.9**, to represent both interacting species:

$$dN/dt = r_0N - aNP$$

$$dP/dt = \chi aNP - \delta_0 P \qquad \text{(Eq. 11.14)}$$

where N and P are, respectively, the population densities of the focal victim and its enemy (predator or parasitoid), r_0 is the per-capita rate of population growth of the former in the absence of attack, and δ_0 is the per-capita rate of decline of enemies lacking victims. Then, a and χ are constants of proportionality, a from a linear functional response (Section **10.2.3.9**, below), while χ relates the number of victims attacked to the number of new enemies introduced per unit of time. Deaths of victims from other causes (caveat 10) are not modelled (Holling, 1973), and while host defences are rarely considered (Gross, 1993; Sections **8.2.2.1** and **10.1.2**) they usually improve with age. To repeat, differential effects of weather are not considered. While the model is somewhat unrealistic (Turchin, 2003), it still tends to produce the wide fluctuations in the densities of the interacting species held to be inherent. It can be rewritten in a compact form:

$$N^{-1}dN/dt = r_0 - aP$$

$$P^{-1}dP/dt = -\delta_0 + \chi aN \qquad \text{(Eq. 11.15)}$$

in which the per-capita rate for each species depends only on the density of the other, namely mutual density dependence. Then, greater realism can be achieved by introducing a Verhulst factor:

$$dN/dt = r_0N\left(1 - N/K\right) - aNP \qquad \text{(Eq. 11.16)}$$

embodying the idea that growth of the victim population is likely to be density dependent in relation to a carrying capacity, K, so yielding a more constant dynamic.

Nicholson and Bailey (1935) developed discrete equations on different principles. While parasitoids search independently and randomly in a homogeneous arena, each female during its reproductive life covers a given area a, its '*area of discovery*', a concept leading to *lifetime track* and *individual searching capacity* (Section **10.2.4.1**). It lays a single egg in every host discovered, but may superparasitize them. The equations then become:

$$N_{t+1} = N_t \exp\left(-aP_t\right) r_0$$

$$P_{t+1} = N_t\left[1 - \exp\left(-aP_t\right)\right] q \qquad \text{(Eq. 11.17)}$$

where the exponents model the effects of overlap between the areas of discovery. Their mathematical justification comes from the kinetic theory of phase transformation, the Avrami Theorem (Avrami, 1939; Mulder, personal communication). An assumption in these models is that attacks are limited by searching time (*time limitation*) (Jervis *et al*., 2008), a principle having particular currency when bad weather limits parasitoid activity (Sections **5.3.1.2**(**h**), **10.2.5.1** and **11.2.2.4**), but is rarely modelled (Rosenheim, 1999b).

Holling (1959a), following Solomon (1949), pointed out, also obvious with the clarity of hindsight, that in assessing a predation rate, in addition to a '*searching and finding time*', there is a '*handling time*' (h) (Section **10.2.3.9**) in which the predator subdues, kills and eats its prey. So the functional response is a double rate: the mean number of prey killed *per* individual predator *per* unit of time (Turchin, 2003). A similar rationale applies to parasitoids. Clearly, as prey density rises so would the encounter rate, but handling time should remain constant. A victim's concealment increases searching and finding time, its defences increase handling time. Models must also recognize the limit to the rate at which a predator's alimentary system can process food (Section **11.5.1**). Even so, predators can be digesting while searching. Other complications arise from the density of the enemies themselves. If the density of parasitoid females were high, interference between them might well occur, as they are affected by the presence of others, as in *Rhyssa* (Section **8.2.2.5**(**l**)). This leads to 'wasted time' (w) due to antagonism since, apart from social species, co-operation in insects is rare. This could be added to handling time, but it would increase with the predator's density, not be constant.

In the continuous model of Rosenzweig and MacArthur (1963) we have:

$$dN/dt = r_0 N\left(1 - N/K\right) - cNP/\left(d + N\right)$$
$$dP/dt = \chi cNP/\left(d + N\right) - \delta_0 P \qquad \text{(Eq. 11.18)}$$

which adds a hyperbolic functional response to Volterra's model, plus some of the tenets of Holling's work. The new factors are c, the maximum rate at which victims are killed or parasitized, and d, the half saturation constant, defined as 'the prey density at which the killing rate is half the maximum'. See Turchin (2003, pp. 79–93) for a fuller treatment.

Apart from the caveats above, several models of parasitoid searching have been called further into question by the remarkable demonstration that the ichneumon *Hyposoter horticoler* has a sophisticated spatial memory (van Nouhuys and Kaartinen, 2008). Females use anticipatory searching, finding most of the egg batches of its butterfly host in the habitat, remembering their positions, and then parasitizing a proportion of them at the appropriate time. Its population size, barring accidents, is a fixed fraction of that of its host (van Nouhuys and Hanski, 2002), not simply density dependent. Learning *per se* in parasitic wasps (Arthur, 1966; Taylor, R.J., 1974; Papaj and Lewis, 1993; Ueno and Tanaka, 1996), in predatory wasps (Baerends, 1941; Evans, 1970; Section **8.2.2.1**) and bees (Michener, 1974; Gumbert, 2000) is well known. Associative learning increases the searching efficiency of polyphagous parasitoids (Wardle and Borden, 1985). Another facet of searching is time allocation to host patches. The pteromalid wasp *Halticoptera laevigata* searches indiscriminately for its host, the tephritid fly *Myoleja lucida*, in honeysuckle fruits. But it spends much less time on fruits that it has searched before (Hoffmeister and Gienapp, 2001), so conserving its efforts.

Grazing systems, being resource/consumer based, have a similar theoretical framework to those above. Thus, the Rosenzweig–MacArthur equations (**Eq. 11.18**) may be re-deployed using appropriate symbols. But unless further assumptions are made, this leads to widely fluctuating results, quite unlike grazing in nature. This is because these models assume that all the vegetation is available to herbivorous insects, whereas in reality only a proportion is vulnerable: mostly they attack only roots, *or* leaves, *or* reproductive parts (Section **2.3.2**). Turchin and Batzli (2001) modified the Rosenzweig–MacArthur equations to take account of this:

$$dV/dt = u_0\left(1 - V/m\right) - aVN/\left(b + V\right)$$
$$dN/dt = \xi N\left(aV/\left(b + V\right) - \eta\right) \qquad \text{(Eq. 11.19)}$$

where V is the density of plant biomass, N is the population density of grazers, u_0 is the linear rate of regrowth of the vegetation when $V = 0$, m is the carrying capacity in the logistic term, η is the intake by herbivores when their population shows zero growth, and ξ is the conversion rate of biomass from plant and insect. In reality, food quality shows great variation, while plant patches may grow away from herbivores, whose numbers are often held down by other factors. Andrewartha and Birch (1954) pointed out that some of a prey's population might be unavailable to a predator (often because they are in a refuge, caveat 8 above), just as plant food usually is, their 'paradox of scarcity amid plenty'.

Even in the laboratory in constant physical conditions it has often proved difficult to get the linked cycles predicted by **Eq. 11.17**. Two of the best fits were: (i) the bruchid beetle *Callosobruchus* and the parasitic wasp *Heterospilus* (Utida, 1957); and (ii) another stored-products pest *Ephestia* and the ichneumon *Venturia* (Auslander *et al*., 1974; Section **6.3.1.2(q)**). In larch budmoths, where population cycles are marked (Section **5.2.1.4(d)**), a tritrophic model including the effects of food quality and parasitoid action gives the best fit (Turchin, 2003). Cycling numbers of the moth *Epirrita*, which defoliates birch in Finland, may be driven by fluctuations in induced chemical defences in its food plant, which remain elevated for 3–4 years after the initial attack (Haukioja, 1980; Section **2.4.2**). But its numbers are acyclical in Switzerland (Berryman, 1996). Then some models (Kaitala *et al*., 1996, 2001) indicate that cycling may arise from random perturbations.

Discrete models, originating from work by Nicholson and Bailey in the 1930s (**Eq. 11.17**), exist for the interaction of predator and prey. But this model may lead to unstable, diverging oscillations. Beddington *et al*. (1975) corrected the problem by adding a self-limiting term to the prey equation:

$$N_{t+1} = N_t r_0 (1 - N_t/K)\exp(-aP_t)$$
$$P_{t+1} = N_t(1 - \exp(-aP_t)) \qquad \text{(Eq. 11.20)}$$

Recently, Hirzel *et al*. (2007, below) have used the Nicholson and Bailey equations to model the spatial dynamics of host and parasitoid in a heterogeneous landscape.

I include these models because they have become part of the theoretical subject matter, not because I believe that the results have very much to do with what happens in *most* natural populations (Pielou, 1981; Hawkins and Cornell, 1994; Rosenheim, 1998; Section **9.4**), largely because of what is left out. After all, in numerous species with sparse populations they would be hard to detect. But they could represent core processes in dense populations as in pest insects under benign physical conditions and so be of economic interest. What is more, they may help to explain what occurs in those rare but spectacular cases of periodic pest outbreak, as in larch and spruce budmoths. Here, regularity of cycling forces even sceptics such as myself to believe that they may result from innate cyclicity, by climatic oscillation (Pollard, 1991; Hawkins and Holyoak, 1998) or even the result of a chaotic process. And there is a distinct possibility that innate cyclicity occurs in other species but is *obscured* rather than *driven* by exogenous factors. Ostensibly linked predator/prey cycles exist in several tropical situations (Godfray and Hassell, 1989). Even so, these could be driven by exogenous factors since the tropics are rarely aseasonal (Section **2.2.3.2**). Again, synchronous cycles in European winter moths (Roland, 1998), some North American forest moths (Miller and Epstein, 1986; Myers, 1998; Hawkins and Holyoak, 1998), similar cycles in separate populations of *Anthocharis* (Courtney and Duggan, 1983) and two Dutch carabid beetles (van Dijk and den Boer, 1992) also seem to be driven by weather. Weather may be an ultimate cause in snowshoe hare/lynx cycles (Pielou, 1981). Perhaps in some cases we have been reading causation the wrong way round (Hawkins, 1992; Section **12.3.1**), so that in reality we may have:

Weather → Amount of and access to plant food → Numbers of herbivores → Numbers of enemies

Apart from the 12 caveats listed previously, has anything been left out? A glance at Thompson's (1943) parasite catalogue, Bushing's (1965; Section **4.2.1.2(h)**) list of bark beetle parasitoids and data for forest moths show that it is rare for a parasitoid to have but one host (Askew and Shaw, 1986; Shaw, 1994; Freeman and Ittyeipe, 1993; Holt and Lawton, 1994; Nair, 2007, his Fig. 10.37). Or indeed, vice versa (Bushing, 1965; Freeman, 1981a; Askew and Shaw, 1986; Gröbler and Lewis, 2008). Monophagous predators are rare. Then, parasitoids usually attack a specific stage of the host(s): egg, small or large larva, pupa, even the adult. Being selected to maximize their RS, they often *feed on and kill* smaller hosts but *oviposit in older, larger ones* (Section **8.2.2**). This and other effects caused by food, or lack of it, greatly influence parasitoid field dynamics (Jervis and Kidd, 1986). Offspring in large hosts often survive better, develop faster and become more fecund (Murdoch *et al*., 1998). A parasitoid's sex ratio may be male biased in small hosts, while a range of enemies attacks the parasitoids themselves (Rosenheim, 1998). In Finland, the ability of *Cotesia melitaearum* (Braconidae) to suppress *Melitaea cinxia*, is limited by the hyperparasitic ichneumon, *Gelis agilis* (Lei and Hanski, 1997). Of course, interactions are often tritrophic (Section **9.1**), even tetratrophic: plant, herbivore, parasitoid and hyperparasitoid. And it does not end there because in plant/aphid systems, ants frequently affect the parasitoids and hyperparasitoids differently (Völkl, 1992; Weisser, 2000).

The problem of the joint action of specialist and generalist predators is addressed in a continuous model by Hanski *et al*. (1991):

$$\begin{aligned} dN/dt &= r_0N\left(1-N/K\right)-cNP/\left(d+N\right) \\ &\quad -gN^2/\left(h^2+N^2\right) \\ dP/dt &= s_0P\left(1-q\,P/N\right) \qquad \text{(Eq. 11.21)} \end{aligned}$$

Here the new parameters are g, the saturation rate in the sigmoid functional response, s_0, the intrinsic rate of population increase of the predators, and h, the density at which the third contribution is at half its maximum value. But again, there is usually a differential effect of physical factors on victim and enemy. Thompson (1929) pointed out that control by enemies:

> is limited by their specific requirements, of which the presence of the host organism is only one. The physical factors … are simply intensities of omnipresent physical and chemical influences above or below the limits between which a given species can subsist.

This leads to differential effects on the interacting species (Burnett, 1949; Weisser *et al*., 1997; see Fig. 10.9 and Section **10.2.1**) and is germane to most temperate and some tropical situations. When it favours hosts, their numbers become unrestrained by parasitoids, for example *Schizaphis graminum* (Section **5.3.1.2(h)**) in the cooler parts of its range. And when gypsy moths in former Yugoslavia defoliate oak trees, *Blepharipa* (= *Blepharipoda*) *scutellata* and *Parasetigena* (= *Phorocera*) *agilis* (Tachinidae) were repelled (Sisojevic, 1975), maybe by increased light and/or reduced humidity. Any restraining influence they had was broken down. When conditions favour the parasitoid, the host may be driven to extinction locally (Section **10.1.1**). In addition, to reveal the reality of nature, population models must express population fluctuations at low density, although as we noted, the peculiarly dense populations of pests are of special interest to us.

As I have often emphasized, natural insect populations are very often unbounded. Redistribution is a major feature of the dynamics of parasitoids and their hosts (Johnson, 1960, 1969; Freeman, 1965, 1976, 1981a; Danks, 1971b; Taylor and Taylor, 1977; Taylor, 1986; Freeman and Geoghagen, 1989; Freeman and Ittyeipe, 1993; Drake and Gatehouse, 1995; Woiwod *et al*., 2001; Walter, 2003; Gripenberg and Roslin, 2007; see caveat 9). Finally, co-evolution may be at work: but would it occur at a rate to influence materially the assumptions of the equations? Co-evolution may be asymmetrical and prey may be more likely to evolve defences than predators can evolve improved attack (Juliano and Williams, 1985; Vermeij, 1994).

In summary:

1. Physical factors limit the number, size and quality of *the places* that a given species may inhabit and in turn the quantity and quality of available food: the *global carrying capacity*, while bad weather limits redistribution.
2. Within such favourable places reproduction occurs only where resources exist in an appropriate spatial pattern (Section **12.3**).
3. The physical environment often acts differently on interacting species.
4. Globally, losses due to emigration are greater and often far greater than gains due to immigration. Thus, migration is a wasteful, and often a very wasteful process (Elton, 1927; Freeman, 1976, 1981a; Taylor and Taylor, 1977; Taylor, 1984; Freeman and Ittyeipe, 1993; Roff, 1994; Ward *et al*., 1998).

For point 4, in the midge *Asphondylia* (Freeman and Geoghagen, 1989), the parasitoid *Melittobia* (Freeman and Ittyeipe, 1993) and the aphid *Rhopalosiphum padi* (Ward *et al*., 1998), the majority of population losses are due to the inability of emigrant females to locate resources (Section **10.2.4.1**). For insects seeking food plants, ‘A truly astronomical number of [individuals] … find themselves on the wrong [plant] … and either leave or perish’ (Strong *et al*., 1984). Many parasitoids have been found flying high in the air (Farrow, 1981), doubtlessly at high risk. *Drosophila* spp., while small, may fly considerable distances (Brussard, 1984; Schiffer *et al*., 2007; Bridle *et al*., 2009). In relation to such risk, the outcome is that the failure to lay a complete compliment of eggs becomes a key factor in lepidopteran dynamics (Dempster, 1983) and those of some other orders (Leather, 1988).

11.5.3 Models including space: Populations in patches

Space (one- to three-dimensions), time and density of one or more interacting organisms may be included in these models, which again can be continuous or discrete. The former are generally easier to solve analytically, but continuous variables must be ‘discretized’ for solution on a computer. This approach has become increasingly relevant to metapopulations. Levin (1976) noted that contemporary mathematical population models had ignored spatial factors, while in that year I addressed the need for a spatial approach to field studies of insect populations (Freeman, 1976). Fourteen years later, May and Southwood (1990) remark ‘... it is becoming increasingly clear that many – and possibly most – species inhabit environments that are patchy in space and variable in time’. Yes indeed: recall that Thompson and Nicholson pointed this out long ago! Even in 2005, Cronin and Reeve lament the paucity of ‘spatially explicit population models’.

To be realistic, models must include space and time (Southwood, 1977). Hassell (1998b, p. 35) notes:

> If all the insects had the same probability of survival, irrespective of the number in their particular patch, the spatial structure of the environment would be largely irrelevant and a simple homogeneous model would suffice to describe the dynamics of the system. Density-dependent survival within patches, however, makes the spatial distribution of individuals important to the survival of the population as a whole.

But the chance of a migrant reaching a new patch, which is often small and dependent on spacing, is a major factor, one omitted in most models (e.g. Hassell *et al*., 1991; Hanski *et al*., 1996), even in some discussions of field results (e.g. Haukioja, 1980). Also peripheral isolates, while sparse, have low survival (Thompson, 1929; Freeman, 1981a). Unless conspecific individuals are close, they cannot interact (Richards, 1961), and time lags may occur. The 'patches' here can be habitats or patches, according to reality, and the models can be related to, or derived from, metapopulation work (Ovaskainen and Hanski, 2004; Hirzel *et al*., 2007). Fragmented habitats are often called, rather ambiguously, 'habitat patches' (Section **12.2**). Models consider single species (de Jong, 1979; Hassell, 1980; Hanski, 1994) and multi-specific situations addressing competition and predation (Levin, 1976; Hassell, 1980; Kareiva, 1987; Comins *et al*., 1992; Hirzel *et al*., 2007).

Although Skellam (1951) produced an early spatial model of a fragmented animal population, one of the best known is that of Levins (1969) which considers changes in the fraction of occupied patches (or habitats), $P(t)$, in an infinitely large network. These changes are given by:

$$dP/dt = cP(1-P) - eP \qquad \text{(Eq. 11.22)}$$

where c and e are the colonization and extinction rates, respectively. This equation shows the classical feature of a metapopulation: its *long-term persistence despite frequent extinction within its component patches* (den Boer, 1968, 1985; Freeman, 1977, 1981a; Hanski *et al*., 1996). But of course metapopulations vary greatly in their level of redistribution, of which patch duration is a major determinant (Section **12.2.3**). While habitat fragmentation is sometimes held to stabilize insect numbers (May, 1978), well-replicated field experiments using an aphid and its coccinellid predator (Kareiva, 1987) show that the specific behaviours of predator and prey are critical. Indeed, in this case more aphid outbreaks occurred with greater fragmentation. Then, a further realistic refinement is to take account of the probability of extinction within a patch (E) in relation to its size, and the probability of the colonization of a patch (C) relative to its isolation (Hanski, 1994). The long-term chance of a patch being occupied (J) is given simply by:

$$J = C/(C+E) \qquad \text{(Eq. 11.23)}$$

Spatial models access work done long ago by physical chemists on particle diffusion, employing either *Lagrangian* or *Eulerian* viewpoints (Turchin, 1998). The first centres on moving particles (= individuals) and is more useful in behavioural studies. The latter concerns a region of space and the probabilities of individuals entering or leaving it, and is more suited for population studies. Even so, after redistribution individuals have chances of finding a patch and of dying in transit (Taylor, 1988; Stamps *et al*., 2005; Starrfelt and Kokko, 2010), chances affected by intrinsic and extrinsic factors. The former is covered in the ISC concept. Extrinsic factors relate to size and spacing of target patches (Hanski, 1998a) and the largely physical vagaries of transit (Section **9.9**). Endopterygotes usually mate before migration (Roff, 1994). But if a migrant female fails to do so, she must mate before she can lay eggs or, unless parthenogenetic or haplodiploid, her efforts are in vain. Some exopterygotes, like delphacid bugs (Section **5.3.1.2(d)**), mate after migration. Mate finding and mating itself take time and with feeding reduce time available for oviposition.

There is often a situation in which individuals are moving out from an area of high population density (Haldane, 1956; Nicholson, 1958), which is applicable to the familiar central/marginal model (Mayr, 1963; Section **12.1**). With random dispersal the situation is like molecular diffusion, except that in terrestrial situations dispersal is confined effectively to two dimensions (Turchin, 1998). Drawing a conceptual line through the dispersing group after time T gives a quasi-normal distribution, which occurs because not only do they move randomly but also spread into an ever-increasing area. The telegraph equation, however, is a better model (Turchin, 1998, p. 89), since it makes the realistic assumption of movement at finite speed and effectively truncates the tails of the distribution (see Taylor and Taylor, 1977). The equation:

$$N = \exp\left(a + bx^c\right) \qquad \text{(Eq. 11.24)}$$

where N is density at distance x from a centre of dispersal, and a, b, and c are parameters, describes several data sets on insect dispersal well (Taylor, 1980). But when movement is through the matrix it often occurs along directed paths, so that the heading at time T_2 is correlated to that at time T_1, making their spread more rapid. Individuals often follow linear features such as rivers, woodland edges and other topographies (Drake and Gatehouse, 1995; Roland and Taylor, 1997; Section **10.2.4.1**). Also, the directional component may be due to diurnal or seasonal winds, or movement in swarms, so that individual paths are correlated. This linear aspect of redistribution recalls the concept of corridors in conservation biology (Simberloff *et al*., 1992). Even if the directions that individuals move are not mutually correlated there is still diffusion, although totally random movement by insects in nature is rare (Taylor *et al*., 1978b; Taylor, 1984).

BIDE models are an early spatial class, so called because they include births, immigration, deaths and emigration (Cohen, 1969). Pulliam (1988) developed these which show that the persistence of a population in which $b < d$ was possible only if immigration made up the shortfall, which is obvious. This is often thought to occur at the edge of the species range (Gaston, 2009b). But they are unrealistic as they assume again that all emigrants find a new habitat, which is intuitively unlikely and from a mass of field data patently untrue (Danks, 1971b; Freeman 1973a, 1976, 1981a; Watmough, 1983; Freeman and Geoghagen, 1989; Freeman and Ittyeipe, 1993; Ruxton *et al*., 1997; Ward *et al*., 1998; Schtickzelle and Baguette, 2003).

To continue, consider a metapopulation with discrete generations, like that of *Apion dichroum*, (N_t) divided into n habitats. Adult females, having survived winter in woodlands (Section **6.2.1.2(a)**) migrate prior to oviposition, finding several clover field habitats with N_i individuals in each. Each female lays F eggs so that initially there are FN_i eggs per habitat. Assuming juvenile mortality is density dependent, S_i, the survivors constituting the next generation of $(t + 1)$ adults is given by:

$$S_i = FN_i \exp\left(-aFN_i\right) \qquad \text{(Eq. 11.25)}$$

the degree of density dependence depending on the magnitude of a. New generation weevils then fly back to the woodlands, where mortality but not reproduction occur (**Eq. 11.5**).

An early model of spatial interaction between two species (Slatkin, 1974) considers the outcome of interspecific competition in scattered, patchy habitats. While both species have probabilities of going extinct in any habitat, irrespective of the effects of any competition, the model permits regional coexistence if recolonization is assumed. Comins *et al*. (1992) examine models of a host/parasitoid interaction where in each generation specified fractions of each species within each habitat move to adjacent ones. The models are constrained to nearest neighbour, as opposed to global, redistribution and show a ‘remarkable range of dynamical behaviour’, including spiral waves, spatial chaos, a crystal lattice pattern or extinction within habitats. These patterns are *critically dependent* on the proportions of host and parasitoid migrating (Hassell *et al*., 1991; Weisser and Hassell, 1996; Hirzel *et al*., 2007). Even without density dependence, migration maintains metapopulation persistence and reduces fluctuation of numbers as long as habitats are numerous. In nature, however, insects can redistribute only during favourable weather, while empirical evidence shows that migration is a wasteful process (references above), a fact that is often neither quoted nor modelled (e.g. Hirzel *et al*., 2007). Realistically, Weisser and Hassell (1996) include in their equations the parameter s to cover deaths of parasitoids in transit, and point out that when travelling, which may involve a significant proportion of their population and can be time consuming, they cannot attack hosts (caveat 9 in Section **11.5.2.3**). Such effects reduce the amplitude of population fluctuation in models of dispersal. Similarly, for parasitoids, Hirzel *et al*. (2007) separate the dispersive from the reproductive/parasitic phase in their equations.

Hassell (1998b), reviewing models by de Jong, finds two related situations, which I have simplified: (i) mated, fertile females emerging from each of several habitats exhibit a typical period of undistracted migration (Johnson, 1969) and then select a habitat where each one lays all the eggs; and (ii) such females move between habitats (or patches) depositing a single egg in each one, which is somewhat reminiscent of hawk moth behaviour. It is assumed that females in the first case or eggs in the second will have one of four types of spatial distribution: uniform (unlikely), binomial, Poisson or negative binomial. Hassell modifies one of de Jong’s equations to analyse aspects of the dynamics of viburnum whiteflies (Section **5.3.1.2(c)**):

$$E_{t+1} / n = Fs\Sigma_j jp(j) f(j) \qquad \text{(Eq. 11.26)}$$

where E_{t+1} is the total number of eggs in the next generation, n the number of leaves (patches), F is the net reproductive rate (55 eggs/female) devalued by s, the proportion of these eggs that are actually laid. The latter parameter turns out to be either density independent or density dependent according to the circumstances. Then $p(j)$ and $f(j)$ are the probability of having j juveniles in a patch, and the (density dependent) probability that an egg will survive to become an adult, respectively. We saw that for most Lepidoptera (Section **5.2.1.4**) this is not how females distribute eggs, either they dump the whole lot at the natal site (bagworms, several lymantriid moths) or they disperse undistractedly, and then deposit batches in each of several patches (a large majority).

What matters for the population dynamics, however, is (i) the spatial distribution of the individuals; (ii) the degree of density dependence; and (iii) the AF.

More recent models have centred on metapopulations specifically (Ovaskainen and Hanski, 2004), who point out they are of two types: those based on individuals (IBMs) and those based on the stochastic occupancy of patches (SPOMs), which relate to Lagrangian and Eulerian principles, respectively. Using empirical data from Finland on the Glanville fritillary (Section **12.3.3.2**) they show that both approaches can be unified to cover situations in which individuals exhibit a range of redistributive movement.

There is also the question of self-organizing patterns (Hassell *et al*., 1994). At root these relate to the general principles discussed in Section **9.8**, but here, more specifically, are confined to self-organized spatial dynamics (Rohani *et al*., 1997). They include models in which each patch may take only a finite number of discrete values (cellular automata; Durrett and Levin, 1994), or assume that each site can be real-valued (coupled map lattices; Hassell *et al*., 1994). Although the reality of these models has been questioned, this area of study continues to provide further insights into spatial dynamics.

12 The Dynamics of Insect Numbers 2: Pattern and Process

12.1 General Introduction

Population dynamics is the centrepiece of ecology (Elton and Miller, 1954; Price, P.W., 1997). It concerns the 'distribution and numbers of animals in nature' (Elton, 1927; Section **9.3**). But to study insect dynamics effectively, natural heterogeneity must be brought to order. First, there is *intraspecific* variation. Individuals of a focal species vary in stage, genetic make-up and the results of prior external influences. Second, their environment has several levels of space and more intimately of the distribution of resources and refuges (Sections **9.8, 9.9** and **12.2**), which may or may not be occupied at a given time (Andrewartha and Birch, 1954). Some processes depend on time (diurnal, generational and annual), which influence birth, death and migration rates relative to the areas occupied (Hanski, 1985; Section **12.3**). Age distribution in a population reflects the number of annual generations, which often depends on latitude, the global spatio-temporal driver (Section **2.2.2.1**). So, there are *spatio-temporal resource patterns and dynamical processes*. These patterns, often modified by *ecosystem engineers* (Jones *et al*., 1994, 1997; Section **10.1.2**), determine the *potential spatial distribution of reproduction* in our species. Potential because a harsh climate and chance often prevent perfectly adequate resources from being utilized (see above). *Dynamic processes* are traditionally the time-dependent ones of *births, deaths* and *redistribution* that although take time are also space dependent, relating to pattern and scale (Levin, 1992).

These patterns and processes define the dynamics of a species and promote its evolution (Southwood, 1988; Murdoch, 1994; Andersson and Hambäck, 2012). In sum across species, they influence much of the community and regional structure, while in reverse these influence the fauna at lower spatial levels (Ricklefs, 1987; Gaston, 1988; Cornell and Lawton, 1992), since local communities are made up of species drawn from regional pools. Indeed, influences operate in both directions: patches affect regions and regions affect patches. We recall that natural selection, the evolutionary engine and creator, is a dynamic population process (Haldane, 1956), arising from differential inheritance of individual inequalities *relative* to existing conditions. Extrinsic theories of population (Section **11.2.2**) largely exclude these processes, intrinsic ones (Section **11.2.3**) do not and so are potentially fuller. Population dynamics proceeds on the shifting sands of genetical and environmental variation in time and space. Of course, species and individuals are unequal, some are more *ecologically efficient* (Section **9.8**) than others. Chance (Thompson, 1929; Dempster and Pollard, 1986; Benton *et al*., 2006) and chaos (Schaffer, 1985; Zimmer, 1999) are also players in the game (Section **10.1**).

We will not start with axioms and postulates from the mathematical approach to insect dynamics (Section **11.5**), but proceed from field data, sometimes using deductive models to clarify them. A general theory of insect numbers is far too complex to be expressed only in sets of equations (Schaffer, 1985), although these may be deployed to refine it. As Thompson (1939), a pioneer in their use points out, 'there is … no way of developing a method that can reduce to a manageable [mathematical] form the appalling complexity of natural factors or smooth out their unpredictable irregularities'. This is shown by the simplifications made to develop equations in section **11.5**, *even though* they describe only sub-sections. Turelli *et al* (2001), after Gavrilets (1999), regarding complexity in speciation remark, '… mathematical theory is subordinate to verbal theory and generalisations about data'. Models, while precise, are limited and simplistic; verbal descriptions have greater explanatory power but are complex and potentially ambiguous (Wilson, 1983; Rieppel, 2004). Ambiguity arises at two points: (i) writers putting ideas into words; and (ii) readers translating these words into ideas. Both errors can be minimized: the first by careful writing and perhaps erecting null models (Antonovics and van Tienderen, 1991), the second by careful reading. In particular, the reader and in dire cases even the editor may read established theory into a data analysis when the writer is saying something original. Errors cannot be eliminated. Mathematical symbolism avoids this and equations can be visualized in graphs in which deductive and inductive data can be compared. Writing is essentially linear in structure, while the processes we try to describe may be a multidimensional block of complexity. Thus, flow diagrams like Fig. 12.1 are more realistic descriptors that avoid the linearity of the written sentence.

While laboratory experiments on interacting species have been and are useful in revealing the core of dynamics, they lend themselves better to comparisons with models (Pielou, 1981; Schaffer, 1985). But in nature, great complexity may occur when species use and move between different resources in different habitats and are attacked by several enemies in a fluctuating physical environment. How shall we proceed in this changing spatio-temporal world? As above, one may use graphical forms (Figs 12.1 to 12.3), which may be based on mathematical models or on empirical data. They can present a global or, more restrictively, a metapopulation perspective that applies to a multitude of situations. Like the graphical forms of Andrewartha and Birch's (1954) theory (see their Figs 14.6 to 14.9), Southwood and Comins' (1976) population landscape (see Fig. 11.11), and Taylor and Taylor's (1977) *population stele* (see Fig. 9.7) they give intelligible models of simple populations, metapopulations and global populations. Harrison (1991) and Harrison and Hastings (1996) give diagrams of different theoretical metapopulations. But what do the empirical data show?

Using the catchy phrase '*distribution of abundance*' (*distribution of numbers* is better although less euphonic), Hengeveld and Haeck (1982) analyse the density of several *global populations* drawn from studies on birds and carabid beetles. Both have a strong tendency to be denser in the centre and sparser at the edge of distribution. But the centre receives migrants from all cardinal points (Gavrilets *et al.*, 2000). The tyranid flycatcher *Muscivora forficata* in the USA (Brown, 1984) provides a neat although avian example. Like cases occur in widely distributed *Drosophila* populations (Brussard, 1984), in the cutworm *Porosagrotis* in western USA (Cook, 1924), unfortunately truncated by the Canadian border, and in

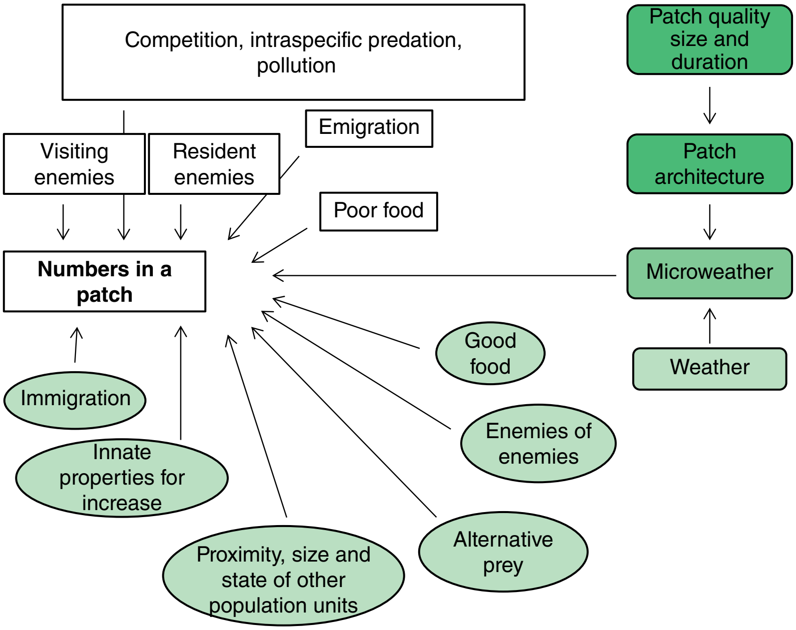


Fig. 12.1. Schematic flow chart of the positive and negative dynamical processes in a population unit inhabiting a patch.

Trypoxylon palliditarse in Trinidad (Fig. 12.2; Freeman, 1981a). Empirical maps of aphid and moth distribution (Taylor, 1984, 1986; see Fig. 12.3) give an insightful display of global populations in space *and* time, and lead to his graphic model of the population stele (see Fig. 9.7). Again, such graphics are halfway between models and verbal descriptions, being less constrained by simplification than the former and unaffected by ambiguity in the latter (Hanski, 1998b; Gavrilets, 1999). Diagrams like Fig. 12.4 can be compared to empirical ones. For field ecologists they may be easier to comprehend than deductive models. We will try to see, however, how such models (Section **11.5**) fit into this diagram and the wide world of observation. In essence, hard but restricted mathematical theory must fit the softer but more comprehensive graphical and verbal population theory.

Such distributions are common (Brown, 1984; Lawton *et al*., 1987), and in population genetics referred to as the *central/marginal model*. Here core areas are usually more genetically diverse than marginal ones (Gaston, 2009b; but see Gilbert, 1980; Harvey, 1996), which brings the intrinsic properties of populations into focus, see an elegantly reasoned paper by Slatkin (1987). Even so, some estimates of heterozygosity using allozyme techniques give scant evidence for its reduction in marginal areas. In *Drosophila*, which is not a famous migrant, but see Johnston and Heed (1976), 'it seems most likely that migration satisfactorily accounts for the lack of geographical differentiation in allele frequencies' (Brussard, 1984; see also Hoffmann and Blows, 1994; Bridle *et al*., 2009). Some of these little flies can move up to 15 km in 15 hours (Coyne *et al*., 1982). Two genetically variable *Drosophila* species along a ~1000 km transect in Queensland, Australia, lack regional differentiation (Schiffer *et al*., 2007). For the mass migrant *Choristoneura fumiferana* (Section **5.2.1.4(c)**), genetic homogeneity exists right across Canada (Harvey, 1996). Similarly, the large, strongly flying moth, *Triphaena pronuba*, has almost invariant proportions of its polymorphic forms across northern England (Bishop and Cook, 1975). In such inquiries genomics is now making an impact (Stearns and Magwene, 2003). In Jamaica, a relatively small but climatically diverse island, juvenile mortality of *Sceliphron* (Section **8.2.2.4(n)**) is low (~20%) at the population edge (Section **11.4.4.3**) where opportunistic migrants breed only during favourable dry weather, so avoiding their parasitoids. Selection is low but migration is high (Freeman, 1977), probably maintaining genetic homogeneity.

For dynamics, diagrams like those above provide a template on which to examine the diversity of processes revealed by field data. Minimally, they

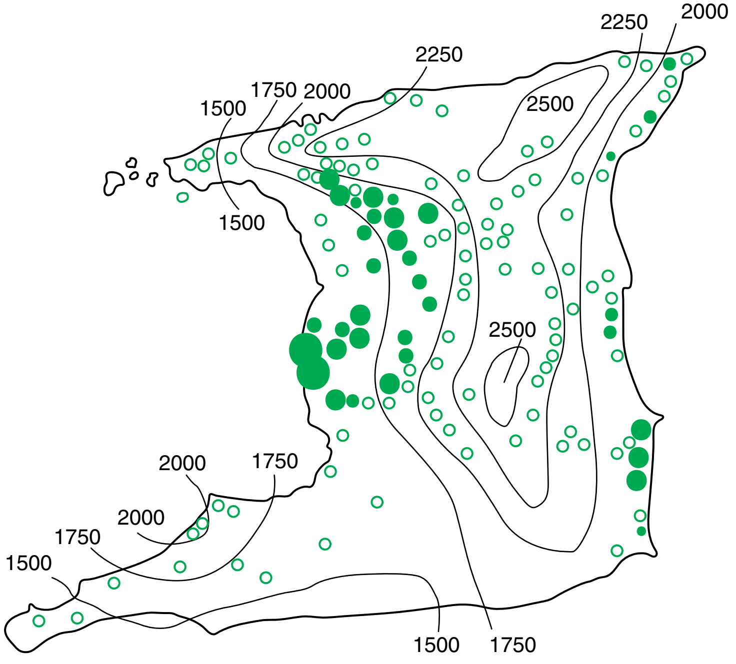


Fig. 12.2. The distribution in Trinidad of the sphecid mud wasp *Sceliphron asiaticum* in relation to mean annual precipitation. A western and an eastern population exist separated by high rainfall in the centre of the island. From: Freeman, B.E. (1982) The comparative distribution and population dynamics in Trinidad of two *Sceliphron* spp. (Hymenoptera: Sphecidae). *Biological Journal of the Linnean Society* 17, 343–360. Fig. 1. Reproduced with permission.

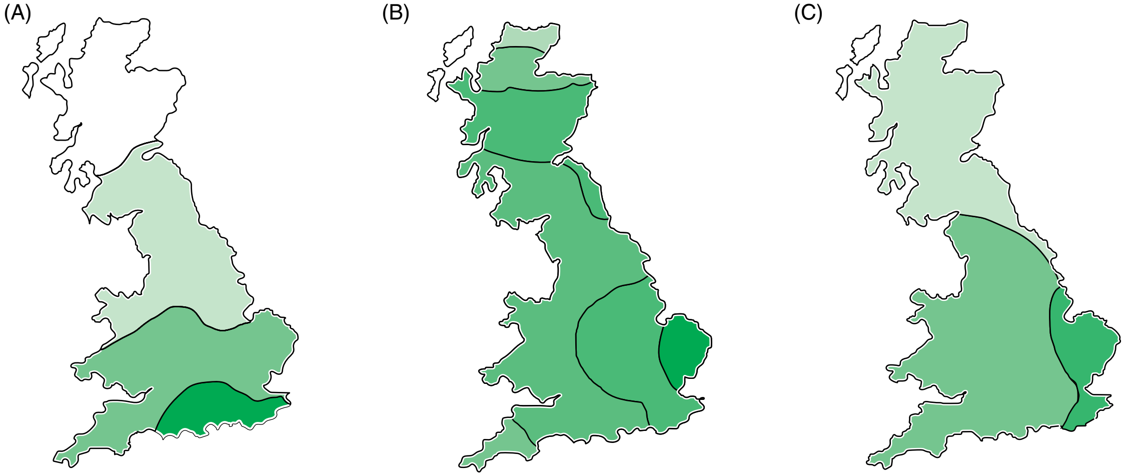


Fig. 12.3. The changing seasonal distribution of migrant *Aphis fabae* in Britain. In spring (A) migrants spread north from overwintering eggs laid on spindle trees on the southern chalk. In summer (B) migrants have reached most of Britain. In autumn (C) further migrants arise from crops in eastern England. Adapted from Taylor (1986) *Journal of Animal Ecology* 55. Fig. 6, p. 19. Reproduced with permission.

involve three spatial levels: *patch, habitat* and *global*. Patch dynamics relates to the immature stages of all species and for a few sedentary ones, like viburnum whiteflies (Hassell *et al*., 1987), gypsy moths (Elkinton and Liebhold, 1990; Section **5.2.1.4(f)**) and some gall midges (Briggs and Latto, 2000), sample much of their global dynamics. For others, because of extensive redistribution (Taylor, 1986; Drake and Gatehouse, 1995), only wide-scale sampling most economically transects through a species' distribution (Whittaker, 1971), can reveal such dynamics (Morris and Miller, 1954; Freeman 1976, 1977, 1981a, 1982; Klug *et al*., 2008). This sums local processes at patch and habitat levels and includes the effects of redistribution. But many similarities between patch dynamics and those at wider spatial levels exist. An aspect is that all births and many deaths are *local processes*, whereas migration is more *regional*. While deaths occur anywhere, they are often concentrated in danger zones (Section **9.9**) far from breeding areas (Freeman, 1981a; Taylor, 1984; Hanski and Gyllenberg, 1993; Ward *et al*., 1998). Generally, global dynamics is enigmatic unless these essential phenomena are estimated through space and time. Wiens (1989) says, 'Our ability to predict ecological phenomena depends on the relationships between spatial and temporal scales of variation'. Metapopulation studies, especially those by Hanski *et al*. depending on adequate distribution, may or may not sample global dynamics but are a giant step in that direction and allow spatial models to be tested. In essence, dynamics proceed when a population of variable individuals within a species interacts with a 'population' of resource patches and reactive organisms that vary in space and time.

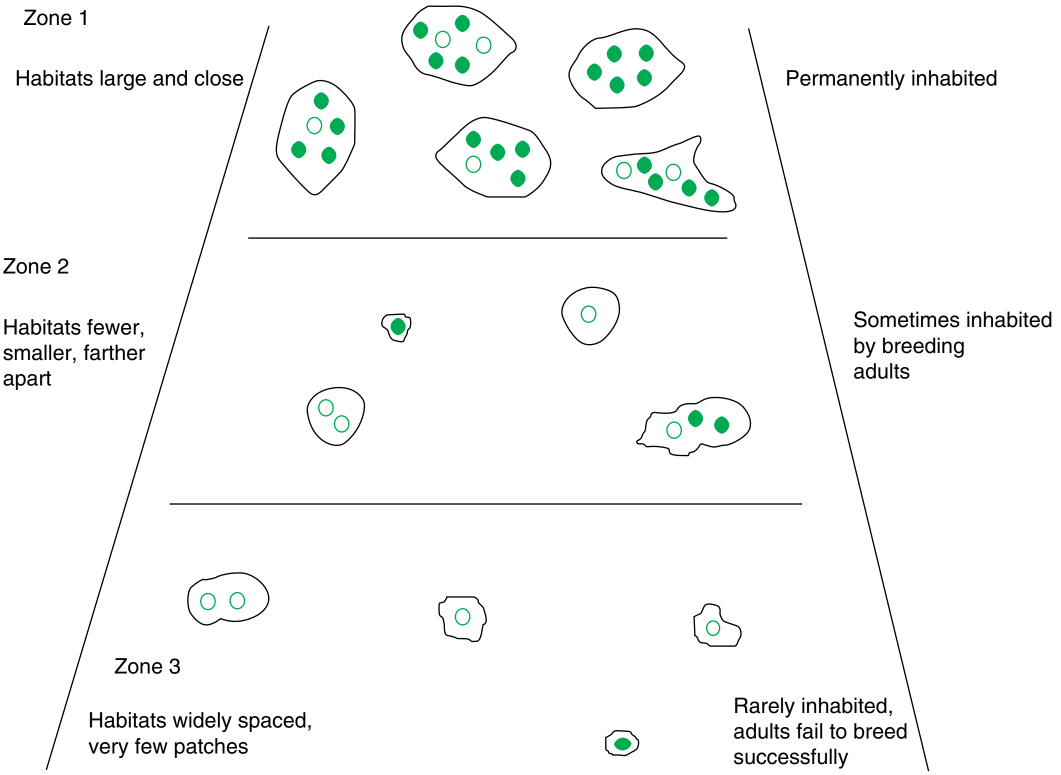
To start we consider the spatial structure of the insect's world: patch, habitat and global, and then the outcomes for dynamic processes at each of these levels. From the inception of autecology, such a structure has been regarded by many as critical to conceptualise insect population dynamics (Thompson, 1929; Andrewartha and Birch, 1954; Freeman, 1976, 1977, 1981a; Freeman and Ittyeipe, 1993; Hanski and Gyllenberg, 1993; Dempster and McLean, 1998). This is also the case in population genetics (Schaffer, 1985; Sugg *et al*., 1996). Such perspectives place local studies of temporal populations in patches (e.g. Varley, 1947; MacLellan, 1977; Hassell *et al*., 1987) in their proper although limited context.

12.2 Pattern: The Levels of Environmental Space

12.2.1 General introduction

Insects have patchy distributions on a range of scales (Andrewartha and Birch, 1954; Freeman, 1973a, 1981a; Taylor, 1984, 1986; Levin, 1992; Section **9.5**). These arise from their intrinsic limitations and

One possible scenario of a species distribution. Large areas represent habitats, black dots and open dots are occupied and unoccupied patches respectively.



An alternative scheme is when habitats and patches do not diminish with distance but a deteriorating climate legislates reducing density

Fig. 12.4. Assuming a global population to be circular the figure represents a large segment. In nature, real global populations will occupy areas of various, often irregular, shapes, as in Fig. 12.2. But in many cases, as here, central habitats are larger and more closely spaced than those towards the periphery. Since the proportion of central habitats occupied is greater and the density of occupied patches higher than peripheral ones, they represent the 'big picture' of a species dynamics (see Section 12.3.4.4).

chance (Thompson, 1929). So the spatial pattern of reproductive resources and legislative action (Section **11.2.2.2**) of physical factors determine the specific *distribution of reproduction*, equating to egg distribution in a given generation (Section **10.2.5.2**). Space near the ground, but outside the habitat, the *matrix* (Ricketts, 2001; Ovaskainen and Hanski, 2004) is not a resource but low-level migration may take place through it. It imposes barriers limiting movement and corridors facilitating it, but is irrelevant for high-level migration which meteorological factors alone influence (Section **10.2.4.1**). Species on the ground are often sensitive to habitat fragmentation (Kareiva, 1987; Schtickzelle and Baguette, 2003). For migratory species, their entire ambit is the *migratory arena* (Drake *et al*., 1995). But the proximity and size of other suitable habitats are critical factors (Janzen, 1968; MacArthur, 1972; Opler, 1974; Hanski, 1994; Goodwin and Fahrig, 2002).

These relationships recall MacArthur and Wilson's (1967) classical theory of real island biogeography. Munroe, plotting numbers of butterfly species on the area of Caribbean islands, first stated this concept in a doctoral thesis at Cornell university (Gilbert, L.E., 1984). Later, he was dismissive of the idea, regarding it as obvious (Vane-Wright, personal communication, 2010). If habitats or islands are closer or larger they are more likely to be found by migrants (Toft and Schoener, 1983). Proximity improves their chances of survival. There may be a central *mainland* population with *island* populations around it (Taylor, 1990; Hanski and Gyllenberg, 1993; Hirzel *et al.*, 2007; Section **11.4.4.3**). There are also '*island ring distributions*' where mountainous interiors confine many insects to coastal lowlands, as in most wasps in Jamaica (Freeman, 1977) and doubtless elsewhere. Then there are *linear populations*, again constrained by topography. Sheltered valleys with streams (Section **2.2.2.2**) have different species from the ridges separating them as in *Dolichopeza* in the USA (Byers, 1961) and *Papilio homerus* in Jamaica. On a wide scale, *Masonaphis maxima* inhabits a strip of the Pacific coast of North America (Gilbert, 1980; Section **12.3.4.2**), although its food plant grows far inland and to the north.

For low-level migrants the matrix provides variable *connectivity* (Ricketts, 2001; Goodwin and Fahrig, 2002). While presenting dangers, it permits adults to distance themselves from enemies and avoid competition with relatives (Starrfelt and Kokko, 2010). On land, low-level migrants can often find water and food, allowing an increased area of resource scanning. But arid areas present a danger of desiccation. If migrants cross water (danger zones; Section **9.9**) risk is high. If they land they usually drown, like my Colorado beetles off the coast of Brittany (Section **5.2.1.2(c)**) and biblical locusts in the Red Sea (Section **5.2.1.1**). While the locomotory capacity of most adults and their juveniles differs greatly, when we consider space (resource space and matrix; see Fig. 12.4), the effectively static environmental template (Section **9.2**), we keep in mind the immense *interspecific* differences in insect flight capacity (Stasek *et al.*, 2008). The big bee *Eulaema mariana* can speed straight over a big lake (Janzen, 1971); the frail little crane fly *Idioptera pulchella* (Freeman, 1968) can drown in a small pool because of a light puff of wind. Dragonflies are more mobile than dainty damselfly relatives (Michiels and Dhondt, 1991). Butterflies have different abilities to navigate the matrix (Ricketts, 2001). Large fritillaries move more, little blues less. Recall (Section **10.2.4.1**) the difference in searching height between large and small pierid butterflies. But there are also *intraspecific* differences in flight capability, either because of size (Dempster *et al.*, 1976), morph or genetic make-up (Watt *et al.*, 2003). Specific predators and parasitoids seeking victims must often pass through the vagaries of the matrix. Redistribution is critical for most but not all insect species (Johnson, 1969; Dempster and McLean, 1998; Desouhant *et al.*, 2003) and an inseparable component of their dynamics.

For food resources, Hassell and Southwood (1978, see their Fig. 1) defined three spatial levels for foraging insects: the *food item*, the *food patch* and the *habitat*. Spalinger and Hobbs (1992) outlined a similar three-level grazing model, which matches ideas on how herbivorous insects *perceive* plants (Prokopy and Owen, 1983, p. 345) and parasitoids their hosts (Vinson, 1984; Jervis and Kidd, 1986; Godfray, 1994). For this ability, *visual contrast*, often in combination with later chemosensory cues, is critical. Contrast implies discontinuity and hence heterogeneity. But habitats are more than a spatial level of a food resource: they are places of generally favourable microclimate in which an *entire and considerable population* may live because they contain *all* necessary resources and refuges (Sections **9.4, 9.8** and **9.9**) in an appropriate configuration.

The concept of fine spatial levels arises from one described long ago by statisticians such as Neyman (1939), that animals in habitats are clumped. Varley (1941) pointed out that randomness relates to spatial scale: what might be random within, say, a patch could be clumped in the habitat. Even so, randomness in nature is rare (Taylor *et al.*, 1978b). Insects are clumped because their food is clumped (Hassell and Southwood, 1978), at least this is a major factor. But *many natural processes, both physical and biotic, result in discrete patches of organic resources*, namely *organic localization* (Section **9.8**). Soils are thinner at the top than at the bottom of a slope, but pockets of highly organic soil also occur. These form, perhaps after a tree is uprooted (Peterson *et al.*, 1990) or a mammal's burrow is abandoned. Thus, many plants exist only in suitable isolated spots.

Insectan herbivores are found at several spatial levels in changing patterns (Thompson, 1929; Taylor, 1986) that are initiated when females seeking food for their juveniles lay egg batches. Young juveniles, lacking much mobility, tend to stay put on the resource patch. So it is inadequate to recognize only habitat versus non-habitat, or to ignore heterogeneity and penetrability (Wratten *et al.*, 2003) of the matrix for low-level migrants.

Hassell and Southwood's three levels of resource space are shown clearly in the distribution of tree-hole mosquitoes, such as *Aedes geniculatus*. Here, food items are small and provide no living space, the larvae being largely filter feeders. Patches are water-filled rot holes that do provide living space and have definite, stable boundaries in the woodland habitat. They can contain hundreds of larvae and persist through many generations. Similarly, in the Neotropics, rain-filled bromeliads provide stable patches for specialized species such as *A. walkeri* (Muddle, 1993). The distribution of tansy aphids is also at three levels: the shoot, the clump and the plant's habitat (Weisser, 2000). Winter moths (Section **5.2.1.4(g)**) are at first sight similar. Oak leaves are food items and large enough to provide living space, oak trees are patches in the woodland habitat. But applying our natural history knowledge, reality is more complex: (i) the leaves are in little bunches on (ii) the twigs, which are borne on (iii) several branches and then (iv) several limbs on (v) the oak tree. Oak trees (vi) are unevenly distributed in (vii) woodlands and usually mixed with other trees. The woodland habitats are clumped in (viii) the landscape (Section **9.3**), being more frequent on topographies that would be difficult to plough, such as steep slopes. Clumped objects form *contagious distributions*, its resource distribution being a *multiple contagion*. Its juveniles navigate multiple spatial levels to reach their food and other resources. But winter moths are not confined to oaks, nor are oaks confined to oak woodlands. Three levels of natural space provide a minimal starting point but do not meet all cases. A 'nearly endless spectrum of spatial scales' (Wiens, 1976) exists. So field carrying capacities may be viewed along such a spectrum. Patchiness is most complex in forests because it occurs in horizontal *and* vertical patterns (Ovington, 1962; Smith, A.P., 1973; Section **9.5**).

While spatial levels relate to the distribution and numbers of all smaller spatial units within larger ones, the general validity of the *patch concept for insect ecology arises from the limited mobility of the juveniles* (Southwood *et al*., 1974) plus the *specific needs of all the instars* (Thompson, 1929). Patches provide a descriptive format of habitat heterogeneity. For a focal predator they comprise groups of victims, who often shares with its victims adaptations to the spatial units provided by plants; for example, to shade, shelter and stabilized hygrothermal conditions in forests, but to exposure, high winds, low temperatures and all-pervading acid moisture on moorlands. Detritivores often inhabit very heterogeneous patches (Section **8.2.4**).

So a patch is the smallest unit of space within which the *innate attributes* of a focal species, leading to its reproductive strategy (RS), can be expressed and its individuals interact. It is a *contiguous area of necessary resources big enough to support the innate attributes of a number of interacting, conspecific individuals*. These comprise *a population unit* (den Boer, 1982, 1998). Indeed, excepting congregation (Taylor and Taylor, 1977), *patches are the only places where increase can occur*. Reproducing adults usually move between them, rarely females do not, as in sedentary bagworms. Patches vary in size absolutely and relatively. At one end of the scale the population unit may comprise a few hawk moth larvae, a fraction of a female's progeny, on a vine. They stay only as long as they take to grow and emerge, since all the adults emigrate. Other species in large patches may persist for several generations and disappear only when deaths exceed births. Hence, suitable patches like suitable habitats *may* or *may not* be inhabited by our species (Spencer, 1864; Thompson, 1929; Slatkin, 1974; Holt and Barfield, 2009). At one end of the scale, hawk moths exist in many small, widely separated and effectively ephemeral patches. At the other thousands of winter moth larvae on an old oak tree are the progeny of hundreds of females and persist for many generations, a difference having basic outcomes for their population dynamics. But for both, since larvae feed on the plant and pupation takes place in the soil under it, these two media must be included in the patch as necessary resources. Patches are often heterogeneous for feeding and pupation. Elton and Miller (1954) include soil structure in classifying habitats. Indeed, close ecological links exist between soil and surface biota (Section **10.1.1**). They also recognize patches (trees, dead wood, dung, etc.) grouping them as 'components of the general system'. For 'components' read patches.

If resources and refuges are clumped, not just food, it refines the habitat concept and gives insight into the spatial structure of the insect's world and its influence on their physiology and behaviour. In patches, the resources needed by juveniles must be close since they have limited mobility. Then for endopterygotes, food without pupation sites would be an inadequate patch. Exopterygotes in general do not need such sites but may require specific places for ecdysis. A species' biology evolves in relation to the spatio-temporal nature of food patches, as Southwood (1977) promoted for habitat. For herbivores this is a reason for using the term *host* *plant* (but see Section **1.5**). Larvae about to pupate and adults about to oviposit must have suitable behaviours to seek and find pupation and food media. *Lymantria dispar* larvae having fed on oak leaves seek crevices in the deeply ridged bark as refuges for pupation. But for *Stauropus fagi* (Notodontidae), feeding on leaves of smooth-barked beech, such crevices are effectively absent. Its larvae, however, spin tightly woven cocoons in which to overwinter between the rot-resistant leaves (South, 1920/1923). *Callosamia promethea* draws a tree leaf together around the cocoon and anchors this leaf with silk to the twig (Comstock, 1940). In autumn, *Limenitis camilla* larvae attach *Lonicera* leaves, within which they hibernate, to the stem (Pollard, 1979). Such behaviour avoids the increase in density attendant on pupation in more localized sites (see Section **10.2.1**).

The structure and microclimate of the patch itself may be critical. *Liriomyza commelinae* (Agromyzidae) selects shaded patches of water grass to lay eggs, never those exposed to sunlight (Freeman and Smith, 1990). The diurnal moth, *Zygaena loti* (Zygaenidae), prefers bare soil and low sward around its food plant, *Lotus corniculatus* (Ravenscroft and Young, 1996). The woodland butterfly *Pararge aegeria* also oviposits more often on grasses isolated near bare soil, where the microclimate is warmer (Shreeve, 1986). Similar effects exist in salt marsh aphids (Hacker and Bertness, 1996) and the swallowtail *Battus*. Selection may occur if food plants are more easily found when against contrasting soil (Section **10.2.4.4**). Analyses of resource use by related grasshoppers (Joern and Lawlor, 1980) properly include *microhabitat*, the micro-environment around food as well as the food itself. This is congruent with the patch as an inclusive unit. But the spatial level of food *item*, aside from adequacy and unlike larger levels, has less interest for dynamics because there must be sufficient numbers of our species (Harcourt, 1969). In general, we can consider the patch, habitats separated by the matrix, and the topography of the landscape as our basic spatial hierarchy.

In most groups juveniles seek their own resources in the patch once their mother has oviposited there, but in most parasitic Hymenoptera all *resource finding*, and in the Aculeata all *resource gathering as well*, has evolved to be a female affair (Malyshev, 1968; Gauld and Bolton, 1991). In solitary aculeates, mothers select the nesting site, build cells for the progeny and provision food from the surrounding area. In this case, 'patch' is a limited spatial level: use 'habitat'. This can embrace 600 hectares in *Sceliphron* (Freeman and Johnston, 1978a; see below) and much more in euglossine bees (Janzen, 1971). The sedentary larvae cannot co-operate or choose either the amount or the quality of their food. The mother, with her developed individual searching capability (ISC), is their food provider thereby acquiring a determining role in their fate. Indeed, the amount of food provisioned for each female larva of *S. assimile* largely determines its adult size and achieved fecundity (AF) (Freeman, 1981b). This type of investment is common in these aculeates (Malyshev, 1968; Jayasingh and Freeman, 1980a; Raw, 1985; Kim, 1997), and has evolutionary similarities to that in some dung beetles (Klemperer, 1983a; Hirschberger, 1999).

Opinion concerning the levels of resource space varies greatly. Andrewartha and Birch (1984), not referring to Hassell and Southwood (1978), define a patch as (p. 17) the 'locality ... an area that supports, or might support, a local population'. This is pretty fuzzy; one thinks that their 'locality' is something bigger than our 'patch'. But later they state: 'A locality might be obviously distinct from the countryside, as, for example, a carcass, a pond or a tree'. Then Schoenly (1990) and Bradshaw and Holzapfel (1991) refer to structures such as dung pats and phytotelmata as habitats; we would regard them unequivocally as patches. More extremely, Whitham (1980) calls a single poplar leaf, galled by *Pemphigus betae*, a habitat. And so do Arthurs *et al.* (2004) for other leaves, and Hausmann *et al.* (2005) for single apple fruits. These would correspond to Hassell and Southwood's food items! Hastings and Wolin (1989), without comment on what has gone before, think of patches as anything from a single plant to an oceanic island! But this may be a valid simplification in a mathematical model, not a real world description. Denno and Roderick (1990) get it right by calling clumps of *Spartina* grass 'patches' for plant hoppers, as do Briggs and Latto (2000) defining *Baccharis* bushes as patches for the gall midge *Rhopalomyia*, and Gavrilets *et al.* (2000) do so in an evolutionary context.

Petit *et al.* (2001) term a 1 km series of small fields along a river 'habitat patches' for the bog fritillary butterfly. This could mean 'patchy habitats' or 'patches in habitats', illustrating the principle that in a quest for *brevity* we may lose *clarity.* For metapopulations the term is often used with the former meaning (Hanski and Gyllenberg, 1993; Hanski, 1998b). But the existence of patches in such habitats is often ignored. A 'fragmented habitat', a term used by Turchin (1998, p. 281) and originally by Thompson and Nicholson (Section **11.2.2**), is consistent with our usage. In Petit *et al.*'s (2001) study, the high level of flight by butterflies between fields resulted in their significant interaction within the system, conforming to Richards' (Section **9.5**) and to den Boer's (below) definitions of population. In bark beetles another tripartite division of resource space occurs: tree, stand and forest (Coulson, 1979). Holling (1992, his Fig. 1) plots a *time/space* continuum for boreal forest chopped up, effectively, into five groups: leaves, tree crowns, patches, forests and landscape. In searching parasitoids, Van Alphen and Vet (1986) use food items (hosts), microhabitats and macrohabitats. While workers describe similar entities, different names may be used, often without qualification. We are left to interpret. Landscape (Section **9.3**), however, is an increasingly useful term.

When we demarcate two adjacent spatial levels, say habitat and non-habitat (matrix), three regions are implied: habitat, non-habitat and *boundary* (Elton and Miller, 1954; Wiens *et al.*, 1985; Stasek *et al.*, 2008; Mair *et al.*, 2015). The boundary, relating to the perimeter/area ratio, will be relatively greater in smaller habitats and in elongate as opposed to more compact areas. An insect's behaviour at the boundary may well be different from that in other places (Hassell and Southwood, 1978). It is an 'observer' (Levin, 1992). In the UK, the woodland crane flies *Austrolimnophila ochracea*, *Limonia nubeculosa* and *L. flavipes*, if carried several metres into an adjacent field and released, fly back directly to the woodland. If released in woodland they fly in any direction (Freeman, 1968). Similar results were found for bush crickets (Kindvall, 1999), the butterflies *Pieris virginiensis* (Cappuccino and Kareiva, 1985), *Euphydryas editha* (Harrison, 1989) and *Speyeria idalia* (Ries and Debinski, 2001), and the passalid beetle *Odontotaenius disjunctus* (Jackson *et al.*, 2009). These observations comfortingly demonstrate that not only are these spatial divisions recognised by the ecologist, but also by the insect. But boundaries add further complexity to already complex spatial levels.

Den Boer (1977, p. 23) following Richards (1961; Section **9.5**), defined a carabid population as an '… *interaction group*: a group of individuals living in a place with spatial dimensions that do not substantially exceed the distances normally covered by the individuals in the relevant patterns of activity, during their lifetime'. Without interaction, individuals could not behave as they must in populations, itself suggesting that their distribution will be patchy (Taylor, 1984). But defining a population by using a behavioural criterion (interaction) makes spatial levels secondary. Then, since interaction usually includes reproduction this is close to what population geneticists term an *ecological deme* (Wilson, 1977) or simply a '*deme*', a localized group freely sharing genetic material (Pielou, 1981; Wright, 1982a; Mettler *et al.*, 1988).

Juvenile interactions exclude reproduction and, as we have seen, usually occur within smaller scales than do those of adults. Dung fly (*Scopeuma*) maggots are confined to dung pats, while the adults roam the pasture and its margins where they feed and mate. Den Boer's definition reflects his idea that 'population' is an 'opportunistic working unit'. Since his carabid beetles are not confined to a patch, but are polyphagous predators roaming habitats in search of various prey, it is fitting for them. So, the concept of patch for hunting adult beetles and wasps such as *Sceliphron* and *Zeta* is unhelpful, although habitat can be. Appendix A in den Boer (1977) shows that his Dutch beetles are usually habitat specific. The terms *microhabitat*, *landscape*, *locality*, *fragmented habitat* and hence *metapopulation* are labels for suitable application.

Patches and population units are *relative* not *absolute* concepts (Section **9.2**), ones relative to the ecology of the focal species. Since the multiple contagion of resources is often not limited to three levels, our choice as to what constitutes a patch may with advantage be 'opportunistic', as are 'populations' (den Boer, 1998). He remarks (p. 76) '… such units of population are better too small (e.g. within patches) than too large'. We choose what is convenient. Thus, Hassell *et al.* (1987) use 'population' for whiteflies breeding on a single viburnum bush. This relativity must be remembered in comparing species and situations. It fits well with the relative nature of patches but needs definition in models. While we discuss habitats and populations we often work on population units whose numerical stability and persistence is normally less than those of proper populations (den Boer, 1968; Tscharntke and Brandl, 2004). Hanski and Gilpin (1991) define several of these terms for metapopulations. Baguette and Stevens (2003) conclude that local and metapopulations are practical concepts. But dividing a habitat into patches is complex as they vary in size, shape, and spacing, and complicates the definition of commonness and rarity. There are now three variables: (i) the number of patches; (ii) the number of individuals per patch; and (iii) the proportion of patches inhabited (Hanski, 1991). The second variable is like Andrewartha and Birch's definition of commonness (1954, their Figs 14.6 to 14.9; Section **9.3**).

While time in ecology is a simpler dimension than space, it adds further complexity to resource space. Apart from spatial level, shape, extent and distribution, *resources have duration*. From this, one co-ordinating idea has universal generality: *the greater the extent of resource space*, *the longer its duration*. For winter moths, twigs last longer than leaves, limbs than twigs, trees than their limbs and woodlands than trees (see Holling, 1992). Southwood (1977), following Thompson (Section **11.2.2.1**), says that habitats are not immutable 'templates' in the engineering sense, but ones that focal and other species (Jones *et al*., 1997) can modify, *modifications that are likely to be relatively more extensive the less the spatial scale* (Turner, 2000; Section **10.1**).

12.2.2 Habitat structure

The enduring concept of habitat dates from Herbert Spencer (1864; Section **9.5**), Elton (1927, 1966) and Tansley (1935, 1946). Habitats comprise diverse, co-adapted assemblies of resource patches, which offer a convenient spatial level for sampling insect dynamics (Varley, 1947; Clark, 1964; Varley *et al*., 1973; Wiklund, 1981; Groden and Casagrande, 1986; Freeman and Geoghagen, 1989). Habitats are often too large (Addicott, 1978) for this, while food items may be too small to contain a sufficient unit of population, although it may be informative to sample several spatial levels concurrently (Heads and Lawton, 1983; Freeman and Smith, 1990; Hails and Crawley, 1992). For crop pests, patches and habitats are usually simple to define (Section **9.5**). In orchards, sawflies and codling moths attacking fruit provide a good, three-level example: the fruits are items, the trees are patches and the orchard is the habitat. Field crops are effectively single-patch habitats when the plants are close and uniform, as in cereals and lucerne. Agriculture reduces, but not entirely abolishes, natural spatial heterogeneity. But within wheat fields the weed species may be patchy (Macdonald and Smith, 1990).

In forests and woodlands, both canopy and understory trees provide the patches, their degree of separation having effects on their status. In the main, contiguous stands of conspecific trees are frequent in taiga and montane coniferous forests. In temperate regions, almost pure stands of beech, oak and birch exist. There are, of course, great differences between the structure of temperate and tropical habitats, the latter generally being far more complex spatially (Janzen, 1970; Section **12.2.4.2**), less so temporally. At the landscape level, topography, climate and soil largely determine the nature of habitats and of the agriculture that can be practised. For the latter, the agricultural equipment used has a marked effect on field area. Big machines mean that landscape heterogeneity will be on a grand scale in the plains, but they cannot be used in small valleys. Also, fields on plains tend to be square or rectangular, those in valleys to show extended linear features. Field size and shape determine edge effects and affect landscape heterogeneity and connectivity. Measurement of such structure and diversity is another consideration. Burrough (1981) following Mandelbrot (1977) suggested that fractals, which are unconstrained by spatial scale, might be used. Mandelbrot applied them to the British coastline, while Morse *et al.* (1985) employed them at the habitat and lower levels. Weiss and Murphy (1988) used them to describe the micro-environment of foraging caterpillars. Simply, a linear fractal measures the relationship between the straight-line distance between two points and the actual distance between them along an irregular path. Surface fractals could also be measured, which might be useful for comparing landscape topography.

Apart from the *spatial components* we have examined above, *temporal* components (Section **12.2.1**) also produce heterogeneity (Thompson, 1929; Wiens, 1976; Southwood, 1977; Holling, 1992). It is simpler to deal with the latter before examining the intrinsic spatial heterogeneity of patches, considerations that help to explain the diversity and validity of the patch concept. After that we will discuss habitat heterogeneity (Section **12.2.4.2**).

12.2.3 Patches in time and how they vary

How do patches (Fig. 12.5) in stable habitats or landscapes vary in time under changing physical and biotic factors (Southwood, 1962)? What *conditions do they impose on the units of population they may house*? Patch duration can be in *real time* or *relative* to the life cycle of a species (Southwood, 1977). But even in persistent patches breeding may be possible for only part of each year (Section **11.5.2**,

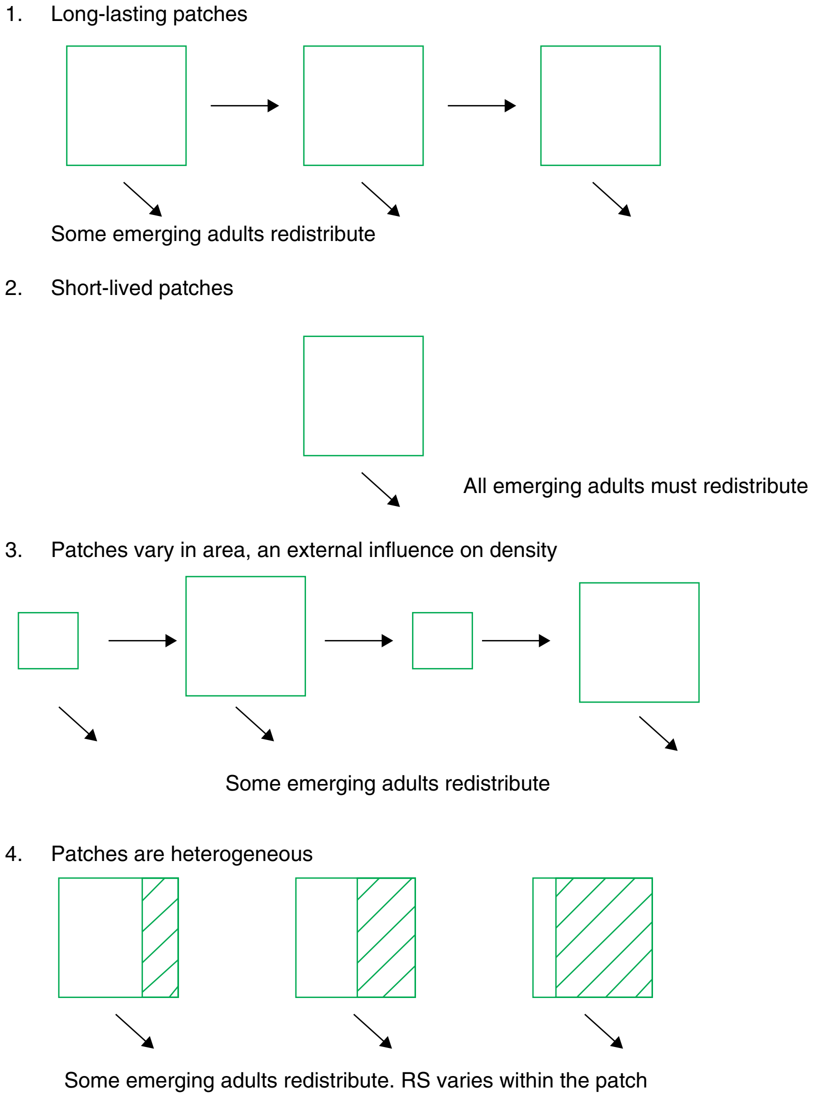


Fig. 12.5. The conditions and effects of patches in time. There are four cases: persistent, ephemeral, variable in size and heterogeneous. Cases 1 and 2 may be the most frequent. RS, reproductive success.

Eq. 11.5). Physical and biotic restrictions exist. In floral pests like clover and apple blossom, weevils (Sections **6.2.1.2**(**a**) and **6.2.1.2**(**b**)), breeding is confined to a brief spring flowering (*biotic restriction*). While summer permits emerged adults to feed, there are no reproductive resources and they survive winter in a separate habitat. Gypsy moth larvae have foliage available on poplars for ~5 months each year, and survive winter as egg masses on trees. Most conifers have foliage all year, but its quality decreases with age (*biotic restriction*) and winter conditions are too harsh for insects to feed on it (*physical restriction*). Patches become unsuitable for breeding for both reasons. The bast of conifers provides a site for bark beetles to feed for much of the year as it offers better protection; even more so for beetles feeding deep in the wood. Predictability is also a factor. Now we look at four, clear-cut types of patch, comparing their effects and restraints on insect dynamics in and between these spatial units.

12.2.3.1 Type one: Persistent patches

These do not change much between years and have rather constant area and spatial distribution. So they are predictable, although food availability and quality usually vary in time. They often comprise trees and soil beneath and underline the principle that *plants often provide more reliable food sources than do animals*. Even herbaceous plants can form long-lasting patches by reason of their clonal habit (Inghe and Tamm, 1985; Callaghan *et al*., 1992). Tamm traced the life of several such patches for ~40 years. Many classical studies of herbivore dynamics belong here: knapweed gall flies, winter moths, codling moths, larch budmoths and viburnum whiteflies. For an insect's *intergenerational strategy,* resources are available *in the same place with roughly the same area* for many years. While these patches may be unsuitable as food for part of the season, they are *predictable in space and time*. We expect some adults to stay and some to leave (Hamilton and May, 1977; Motro, 1983; Starrfelt and Kokko, 2010), the usual strategy for insects on trees in woodlands and orchards, and on other persistent plant patches. Trees grow and get bigger, but at a rate not materially affecting insect density on them, since insect potential to increase is so great (Section **11.5.2.1**; but see Section **12.2.3.3**).

Tree-holes in the seasonal tropics provide long-lasting patches suitable for only a short period after the rains (Fincke, 1992; Becker *et al*., 2010). *Aedes* mosquitoes living in them are adapted to these partly predictable conditions. They spend the dry season as dormant eggs of which *only some* hatch on wetting (Section **7.3.2.4(d)**). Unlike these *Aedes*, Odonata breeding in them pass the dry season as non-reproductive adults. A like phenology occurs in *Nomadacris*. In pests of crops grown repeatedly in one place, as in cereals, sudden changes in plant biomass occur at harvesting. Over time we expect natural selection to adapt their life histories to such crop conditions. Similar local adaptation has been found in careful fieldwork by Mopper *et al*. (1995) on the oak leaf miner *Stilbosis*. Mine initiation was higher on 'home' than on 'new' trees, perhaps because generations of miners had begun to adapt to the defences of their home tree. This would not happen within temporary patches (Section **12.2.3.2**), so there are genetic spin-offs from our patch classification. In field crops, although harvest disrupts continuity, pests may be safely in the ground (wheat midges) or in some snug winter refuge close by (*Apion*, *Hypera*), and attack the same crop again in spring. This suggests that changing crop cultivars to prevent increasing adaptation should provide a useful weapon for integrated pest management (IPM; Speight *et al*., 1999).

In Britain patch use by *Celastrina argiolus* (Lycaenidae) is interesting and unusual. The spring generation feeds on holly (also dogwood and spindle) and the summer one on ivy and bramble, larvae eating the flower buds. The juvenile population alternates between two persistent patch environments, the adults roaming hedgerow and garden habitats. While patches are persistent, they are suitable only at flowering. *Celastrina's* dynamics are more like those of insects in ephemeral patches (cf. *Anastrepha* spp.; Sections **6.3.1.1(l)** and **12.2.3.2**).

12.2.3.2 Type two: Ephemeral patches

These have short duration, change in quality and often allow only one generation of the focal insect to be completed. All emerging adults disperse and seek new resources (Zera and Denno, 1997). These *occur predictably or unpredictably*. Sometimes a few generations can be completed before the patch becomes unsuitable, which thus grades into a type 3 patch (Section **12.2.3.3**). These ideas follow Southwood's (1988), of the 'disturbed habitat' with 'durational instability' although by our definition short duration of patches is not the same thing as changes in the habitats they partly comprise. Such patches often *change* predictably, as with fungal fruiting bodies, but the unpredictability of their *spacing and number* are major factors for the dynamics of insects using them. Unlike the *Celastrina* example, patches come and go at different places in a relatively constant habitat. In some cases, such as dung patches and fungal fruiting bodies (see below) in a meadow, new patches arise near old ones, allowing short-distance movement for seeking them. But the appearance of many ephemeral patches is unpredictable. Patch duration and insect movement are related, as in corixid bugs in ponds (Brown, 1951) and in 35 species of delphacid bugs, in which macroptery, and so the ability to redistribute, are inversely related to patch or habitat duration (Denno and Perfect, 1994). Thus, flight polymorphism is not expected in insects inhabiting ephemeral patches, they must all fly. But unlike permanent patches, their number varies between years as *does the carrying capacity of the habitat or landscape* (see Fig. 14.6 in Andrewartha and Birch, 1954). This variation is only partly predictable and often wholly irregular, as follows.

Partial predictability occurs in patches of annuals springing up in the same place from dormant seeds or vegetative structures. Numbers vary annually, but they exist each summer in temperate habitats, between wet and dry periods in tropical ones, and in deserts after rains. Such plants exhibit rapid growth, maturation, flowering and senescence, with consequent effects on the availability, quantity and quality of food for specific insects. The *Dentaria* food plant of *Pieris virginiensis* (Cappuccino and Kareiva, 1985; Section **10.2.2.5**) is an example. In temperate autumn basidiomycete fruiting bodies occur, develop and degrade predictably. However, some uncertainty does occur (Shorrocks, 1977, 1990), who considered them as patches for species of *Drosophila*. Within cabbages (patches) for *Myzus persicae,* the outer leaves predictably decline in quality and the aphids move to fresher ones or perish (Harrington and Taylor, 1990). Again on a short time scale, tropical fruit flies such as *Anastrepha, Ceratitis* and *Bactrocera* (Sections **6.3.1.1(k)** and **6.3.1.1(l)**), oviposit in a series of fruit species as the season progresses (Atkinson 1985; Fletcher, 1987; Aluja, 1994; Aluja and Mangan, 2008). Like red locusts, Fincke's Odonata (Section **12.2.3.1**) and temperate weevils breeding in flowers, they bridge periods lacking reproductive resources as adults. Temporary pools, in which many mosquito species breed, are a further example, but are predictably numerous and hence more closely spaced in tropical rainy seasons.

For herbivores and most plant pests, the patch concept works well. For detritivores, our distinction of widely distributed, long-lasting phytodetritus from localized and ephemeral zoo- and copro-detritus (Section **8.2.4**) has major outcomes for their ecology. But for predatory insects the patch concept needs qualification. Their food provides no effective living space and is essentially ephemeral. Thus, for enemies of sap-sucking homopteroids the victims, while predictable in time, are unpredictable in space and do not influence microweather. They are collections of food items and hence food patches (Hassell and Southwood, 1978; Heads and Lawton, 1983), but not entire resource patches. The effective patch is completed by the victim's food plant. Such patch complexity is not much different from patches used by many herbivorous insects, where edible leaves are distinct from inedible stems, and where feeding and pupation sites are separate (Section **12.2.3.4**). Coccinellid beetles and syrphine flies use such plants for oviposition, to search for their prey and to pupate (Section **12.2.1**). But mobile predators such as dragonflies, carabid beetles and solitary wasps, roaming through extensive habitats or landscapes, are not patch-specific, any more than are itinerant pierid butterflies and sphingid moths.

Alpine *Zeiraphera* populations (Section **5.2.1.4(d)**) are strongly cyclical, providing variable resources for numerous parasitoids. Such hosts provide a confined living space for parasitoids, drive their numbers (Turchin, 2003) and occur patchily on trees. Similarly, cone production on a pine tree, a patch for *Conophthorus* beetles and so its carrying capacity, varies greatly from year to year (Section **6.3.1.1(c)**). Ectoparasites on small, short-lived mammals provide a further case: they either breed away from the host or have very short generation times (Lundqvist, 1985, in Southwood, 1988). Finally, the presence of patches may be totally irregular in number, size and chronology. Branches decay and drop irregularly (Nye, 1961; Siitonen, 2001) or fall only when high winds, fire or foresters have damaged them. Insects that degrade them live in an unpredictable world (Beaver, 1979; Dempster and Pollard, 1981).

12.2.3.3 Type three: Patches that vary in size

In this case, patches *materially expand or contract* over time and so also *change their carrying capacity*. This may occur during a *single generation* of the focal insect, patch expansion serving to reduce density, reduction serving to increase it, assuming the insect has enough mobility. When no breeding occurs the relationship of population number to population density varies: one might observe the paradox of continuing juvenile mortality and increasing density, namely the number/density anomaly (NDA; Section **9.3**). In a single generation of an insect, a fast-growing annual may increase its size although being eaten by a few insects (Price, 1992). In this case, both plant growth and insect mortality affect insect intensity on the plant.

Patches can change in size and carrying capacity during several generations of the insect. This occurs when a group of conspecific, clonal plants becomes locally dominant and then declines predictably during seral changes. A *Rubus* patch in the gap phase of a temperate woodland, which could support the beetle *Byturus* (Section **6.3.1.1**(**a**)) for say 5 years, is an example. If *population intensity* is relatively constant, *total numbers* rise and then fall. *Tipula paludosa* (Sections **3.2.1.2**(**f**) and **9.3**) provides a less predictable example, one due to the uncertainty of seasonal rainfall. But for locusts in deserts, shrinking patches after heavy rain (due to the passage of the Inter-Tropical Convergence Zone) has fallen are quite predictable, confining the nymphs to a decreasing space and inducing, maybe, a switch to the migratory morph (Section **5.2.1.1**). When such patches are enlarged by reason of favourable weather over extensive areas, the *carrying capacity of the landscape* in which they are embedded also increases (Thompson, 1956; Wellington, 1964), as happens for many mosquitoes after heavy rainfall.

Although larger patches generally can hold a more numerous population unit, *patch quality is an additional factor*. While both promote greater numbers, we must not confound resource area with resource quality.

12.2.3.4 Type four: Heterogeneous patches

Although patches often change in quality *through* time, many exist that are heterogeneous at a *given* time (Section **12.2.1**). Heterogeneity is a matter of degree, may be engineered in large patches (Section **10.1.1**), and is often reflected in the broad adaptability of a species. Several Sternorrhyncha provide cases for a *given time*. Spatially contiguous units of *Eriosoma* (Section **4.3.2**) feed on the roots and bark of apple trees, and may pass from one part of the plant to another (Borror *et al*., 1989), while the grape phylloxera (Section **5.3.1.2**(**g**)) galls both the leaves and the roots of vines. Several scale insect species infest the leaves, twigs and fruit of a single tree. But when a caterpillar feeds on a plant and pupates beneath it such heterogeneity is used *sequentially*.

Choristoneura pinus larvae feed on *Pinus banksiana*, preferring pollen cones to vegetative buds. When cones are few, larval survival is poor and emigration induced (Nealis and Lomic, 1994; Section **5.2.1.4**(**c**)). Then, perennial plants may have a sectorial structure, one largely dependent on their vascular architecture above and below ground (Watson and Casper, 1984; Orians and Jones, 2001). Indeed, many plants, especially large perennial ones and long-lived clones, may be genetic mosaics due to somatic mutations (Whitham and Slobodchikoff, 1981), providing variability. Young shoots are often superior food, making the patch heterogeneous, and competition for them may ensue (Price, 1992). Shoots sprouting after damage may have higher quality than those of undamaged plants (Utsumi and Ohgushi, 2008), while specific parts of a plant may provide refuges (Section **9.9**). Similarly, for parasitoids, part of a host population may be beyond reach (Andrewartha and Birch, 1954; Price *et al*., 1980). Examples are bark beetles (Section **4.2.1.1**(**f**)) under thick bark, *Rhyacionia* larvae (Section **4.2.1.1**(**m**)) in big buds, and *Rhagoletis* larvae deep in apples (Section **6.3.1.1**(**k**)). *Lymantria* egg masses (Section **5.2.1.4**(**f**)) have intrinsic heterogeneity for the parasitic wasps attacking them.

For parasitoids, patches of mixed hosts provide heterogeneity. In Jamaica, *Melittobia* (Section **8.2.2.5**(**p**)) parasitizes *Sceliphron assimile* and three secondary wasp species in its old cells (Jayasingh and Freeman, 1980). *Zeta* makes its cells under over-hanging rocks (Taffe, 1983) and on rootlets dangling from them, a heterogeneous patch for *Melittobia*. *Zeta*'s mortality on rootlets is far less (Taffe and Ittyeipe, 1976). In Trinidad, the case in *S. fistularium* (Freeman, 1982) is similar, patch substratum is heterogeneous. Other cases occur in herbivores. *Choristoneura* larvae feeding on pollen cones are parasitized more often than those on leaf buds. The gall wasp *Neuroterus* is attacked by fewer parasitoid species on oak catkins than on leaves (Price *et al*., 1980). Patch definition is subjective, suiting the case in hand (den Boer, 1977), but the larger the patch the greater the variation expected. Heterogeneity and variation are functions of space, as they are of time (Sections **11.3** and **12.1**).

12.2.4 Patches in space

12.2.4.1 Patches and habitats

Southwood (1977, 1988) drew attention to the spatial configuration of 'habitats', which generally equate to our patches *in* our definable habitats (Section **12.2.2**) or landscapes. They have *spatial extent* (size), *shape* (elongate or compact) and *interpatch distance*. If patches are large and adjacent movement between them entails less risk than if they are small and far apart (Hanski, 1991). Forest beech trees for lobster moths (Section **12.2.1**) exemplify the former, mullein (*Verbascum*) plants along field edges for *Cucullia verbasci* moths, the latter. Other things being equal, small patches contain fewer focal individuals, are occupied less often but also more difficult for a herbivore and its enemies to find than large ones. We expect this to promote stability. A similar rationale applies to habitats. Big habitats usually have a greater number and diversity of patches and lesser edge effects (Elton and Miller, 1954; Goodwin and Fahrig, 2002; Section **12.2.1**). Then, relative to small habitats, we expect dispersal between patches will be more significant numerically than migration from them. But the profile of redistribution (Taylor, R.A.J., 1978, 1980; Murrell *et al.*, 2002; Section **10.2.4.1**) also affects this.

Many insects are *habitat specific* (Mair *et al.*, 2015), while others are not. Crane flies are usually found only in specific, humid habitats and hardly ever seen in arid ones (Coulson, 1959; Byers, 1961; Freeman, 1964, 1968 [Table 2]; Freeman and Adams, 1972 [Table 3]), where they would desiccate. The woodland butterflies *Limenitis camilla* (Pollard, 1979), *Erebia medusa*, and others like *Melitaea aurinia* (Ford and Ford, 1930) and *M. cinxia* (Hanski, 1998a) are specific to both patches and habitats. Day-flying moths such as *Callimorpha dominula* (Sheppard, 1951), *Tyria jacobaeae* (Dempster, 1982) and *Zygaena* spp. (Ravenscroft and Young, 1996, personal observations) are localized too, although we expect *some* migration; see, for example, Goulson and Owen (1997) for *C. dominula* and Zimmermann *et al.* (2011) for *M.* (= *Euphydryas*) *aurinia*.

12.2.4.2 Multiple types of patch in the same habitat

The larger the unit of resource space the longer its duration (Section **12.2.1**). The larger the habitat the greater the probability of *patch* heterogeneity within it. Large areas are increasingly variable physically and support more plant and other species and hence more potential inter-relationships. In Europe, oak woods have large patches of a few dominant trees: oak, beech, hornbeam and ash, which have long duration. Then there are smaller understory trees: holly, hazel, crab apple and elder, some lasting no more than 15 to 20 years. There are also transitory *Rubus* species in gap phases and finally herbs, often with areas of bracken, bluebells, anemones and several grasses. Even in this simplified woodland there are more than 13 different patch types for herbivores, each with several insect and other species. Plant ecologists have long recognized *dominance* in a flora, and thus a scale of commonness to rarity of plant patches. One way to quantify this scale is to estimate biomass density relative to a unit such as a hectare. More recently the term ‘appearance’ (Section **2.4.1**) has been used, while Coyle *et al.* (2005) opt for the well-worn term ‘abundance’ (Section **9.3**)!

Habitats are differently structured for monophagous and polyphagous species. For example, in oak woods *Phytomyza ilicis*, a leaf miner, uses only holly (Heads and Lawton, 1983) but winter moths use several large trees: oak, beech, hornbeam, and smaller ones such as crab apple. For the miner, then, patches are fewer, widely spaced and similar, for the moth they are numerous, larger, closer together and variable. In the tropics *Diatraea* and *Heliothis* moths use maize and sugar cane in adjacent domestic plots. Their dynamics within these patch types may well be different. *Dendroctonus ponderosae* (Section **4.2.1.4(f)**) breeds in both large and small pine trees in a given stand, but cannot maintain itself in the latter (Turchin, 2003), which become *sink patches* within the habitat. Also, carabid beetles feeding on crane fly larvae in pasture would find patches of prey in damp areas, where they would spend more time, the aggregative response (Section **10.2.3.9**), but they would find different tipulid prey in any mossy places. The aphid prey of coccinellid beetles are usually more localized. For polyphagous parasitoids the patches comprise different, often spatially separate, population units of each host species (Askew and Shaw, 1986).

Diversity in tropical forests is usually far greater than in temperate ones. In a transect of 100 trees in rain forest in Mato Grosso, Brazil, Gifford (personal communication, 1967) identified 93 species. Studies revealed 1171 different tree species/50 ha of Malaysian forest (Plotkin *et al.*, 2000, in May and Stumpf, 2000). Naturally, this number is a function of the area sampled, but 300 species/ha could be a fair average for Amazonian forest, about half this for South-East Asian forests, and rather less in West Africa (Nair, 2007). In Europe the figure might be <10. In Panamanian selva up to eight strata exist and conspecific trees, each belonging to one of several hundred species, will likely be far apart (Janzen, 1970). As most herbivorous insects there are monophagous or oligophagous their ability to locate new patches and/or maintain their population units on old ones must be critical. Reference to the species-abundance distribution (SAD) for reduviid bugs from the Mato

Grosso (see Fig. 9.5(a)) shows that many species can exist at low densities. The distributions of herbivores in the forest canopy should constitute metapopulations (Hanski, 1990). Regarding species richness, teak trees, for example, have ~200 associated insect species but great variation exists, 1–188 for trees in Kerala while for *Luchea* trees in Panama the count is >1500 (Nair, 2007). So tropical forests possess tens of thousands of insect species/ha.

Greater complexity in the tropics may exist because organisms have had more time to evolve there (Wallace, 1878; Margalef, 1963), being untroubled by the relatively recent incursions of the polar ice caps into temperate regions. Longer evolutionary time has led to greater biotic complexity, although fossil evidence suggests that this gradient existed before the ice ages (Stehli *et al.*, 1969). In the tropics, extinction from harsh weather should be less frequent (Baker, 1970). We see this trend even within temperate zones where rather few insect species may be capable of enduring cold temperate winters. Their numbers at a given time depend on the balance of speciation and extinction. Possibly under tropical conditions the former has been faster, while for plants intense seed and sapling herbivory near a natal tree destroy its progeny, spacing out conspecific trees and creating opportunities for many species (Janzen, 1970).

Differences between tropical and temperate forests also lie in the received angle and intensity of insolation. The former leads to different tree shapes: broad tops in low latitudes and tall columns in high ones (Horn, 1971; Terborgh, 1985). Trees are adapted to maximize their radiant catch, but many firs in the Alps (46–48°N) form fine columns, perhaps minimizing snow loads. Greater insolation on selva (Section **2.2.2**) results in vines, lianas and epiphytes increasing dramatically, giving greater spatial (Smith, A.P., 1973) and temporal diversity (Strong, 1977). Higher incident energy may cause greater biotic diversity, the *species-energy theory* (Wright, 1983; Rohde, 1992). This occurs within even small regions like Britain (Turner, J.R.G. *et al.*, 1987). Latitude, via insolation, is the *ultimate* physical driver (Section **2.2.2.1**). But less complex areas of tropical forest can occur, as in those dominated by *Mora* and *Eperua* trees in Guyana (Richards, 1963) and *Peltogyne* in Roraima, Brazil (Nascimento and Proctor, 1994). Such forests, however, are associated with poor soils.

In Neotropical forests, insects eating seeds are mainly oligophagous (Janzen, 1970, 1981) with the groups they belong to, such as bruchid beetles (Southgate, 1979), having many species. In Panama, 48% of forest folivores are confined to single plant genera, only 15% being truly polyphagous (Barone, 1998; Section **9.8**). This contrasts with British noctuid moths, many being broadly polyphagous and numerous (South, 1920/1923). So resource seeking for such tropical insects, and by extension for their specific enemies, must be more complex than in forests at high latitude. Mediterranean vegetation is also often complex, like that of the Karoo in South Africa. But broadly speaking, habitat complexity decreases from the selva to the taiga (Section **2.2.3(b)**). Then in selva, biological processes are continuous, whereas in seasonal rain forest and more so in arid, Mediterranean regions and temperate habitats, they show degrees of temporal discontinuity.

12.2.4.3 The 'same' patch considered in different habitats

Can the 'same' patch in different habitats really be the 'same'? For beech, isolated trees had a 35-day shorter annual period of growth than those in forest (Nicolai, 1986). While intraspecific competition for light and nutrients exists, forest associations have mutually beneficial aspects. But an isolated beech tree in a hedge cannot be the 'same' as one in a forest, nor can one in acid soil form the 'same' patch as one in calcareous soil. While all such trees vary genetically, external factors cause further variation. In Jamaica, the eastern population of *Papilio homerus* oviposits only on *Hernandia catalpaefolia* (Garraway *et al.*, 2008). This occurs in virgin and in disturbed forest. Eggs in virgin forest suffered less mortality (47.4%) from the parasitic wasp *Chrysonotomyia* than those in disturbed areas (70.9%). The butterfly's dynamics differ in these habitats, and in the latter might lead to extinction were these beasts not replenished from the deep forest, a further example of a rescue effect in a sink habitat (Freeman, 1981a; Section **9.4**). Patches are comparable, not identical. The conditions they experience are different. Of course, such patches also vary in size. As within heterogeneous patches (**12.2.3.4**), differences in the environment external to the patch lead to differences in the composition, behaviour and dynamics of their insect occupants.

12.2.5 Multiple habitats, single and multiple patches

There are two situations in which multiple habitats are used. First, many species have a breeding habitat during the favourable season and a separate, often adjacent habitat, in which to survive the harsh season (**Eq. 11.5**). Several examples occur in temperate Coleoptera (see below). Second, there are species that use two or more habitats for reproduction. The landscape affects lower spatial levels, and many examples of this occur in different orders. In general, they have good powers of searching (Section **10.2.4.1**) and navigating the matrix.

Examples for the first situation include *Apion dichroum* and *A. apricans* (Section **6.2.1.2(b)**) that breed in fields with contiguous patches of clover but have a winter habitat of woodland with various refuge patches (Freeman, 1965). Colorado beetles (Hunt and Tan, 2000), cotton boll weevils and many Carabidae are similar (Spurgeon and Raulston, 2006), *Bembidion lampros* and *Pterostichus cupreus* adults overwinter in dense grass at the edge of cereal fields (Wallin, 1986), but move to the centre of the crop to forage and breed during better weather. *Amara plebja* breeds in fields and overwinters in woods, orientating their autumnal flight towards prominent silhouettes (van Huizen, 1977). Some coccinellid (Section **8.2.2.4(e)**) and several other beetles behave similarly. Comparably but differently, many holocyclic aphids reproduce in spring on the winter refuge tree and then fly in search of diverse summer food plants and breeding patches. Resources they require in the two seasons are quite different.

In the second case, monophagous larvae of species like the holly leaf miner feed on the leaves of a single tree species in different woodland types, being *multiple habitat single patch* species. Polyphagous species have the plasticity to use multiple patches and breed in several habitats. Thus, many moths reproduce and feed on a *range* of trees in different locations. Gypsy moths attack more than 500 tree species in North America. Blow flies infest various patches of carrion, in fields, hedgerows and woodlands (different habitats), so the physical and biotic characteristics of different patches and habitats vary. Maggots in woodlands develop more slowly, due to lower temperatures than in fields, but as the air is more humid they rarely desiccate. They are *multiple habitat, multiple patch species*. Their regional dynamics have a landscape base rather than a habitat one. These two situations illustrate a telling dichotomy. Insects such as most *Tipula*, *Dolichopeza* and other Nematocera live in specific habitats (Coulson, 1959; Byers, 1961; Freeman, 1968), others like gypsy moths and blow flies are wide-ranging landscape species (Norris, 1965; Brown, 1984).

Apart from winter and gypsy moths, several prominent moths feed on poplars, willows, birch, beech, alder and hazel (South, 1920/1923; Martinat and Allen, 1987) present in a variety of habitats: humid carrs, riverine and less humid woodlands. This diversity should add numerical stability and reduce fluctuation (Levin, 1976; den Boer, 1982, 1998) to the dynamics of these moths. They are never abundant in the UK, but the North American *Heterocampa guttivittata* has outbreaking populations (Martinat and Allen, 1987). Possibly related to this habitat diversity, larval *Pheosia tremula* and *Lophopteryx capucina* are polymorphic.

To expand a little, for insects such as hawk moths, most *Pieris* butterflies (Baker, 1978), and *gregaria* locusts, with itinerant wandering and opportunistic oviposition, and vagrants like many Cicadellidae, Delphacidae and Aphididae, the habitat concept is in question (see Hanski, 1998b). In temperate summers, dragonflies and chafer beetles have feeding and breeding areas far apart. For such insects it is better to conceive patches embedded in landscapes with populations bounded by harsh physical conditions or lack of resources (Johnson, 1969; Taylor, 1977; Section **9.5**). In cabbage fields *Pieris* females fly in, lay a few eggs on separate plants, and fly off, perhaps laying more eggs on nasturtiums in a garden, and so on. The juvenile population in each place is the progeny of a few vagrant females each of whom leave offspring elsewhere. The dynamics of such species are quite different from habitat-specific crane flies or whiteflies tenacious to viburnum bushes (Hassell *et al.*, 1987). Egg distribution is inseparable from the population concept. But *if the habitat concept is not useful, the patch concept remains so*; we conceive patches in landscapes. Thus, the duality of patch and habitat, while not meeting all cases, provides the basic description of the spatial organization of resources for many species. Larger, more numerous, closely spaced patches increase the carrying capacity of natural habitats and landscapes. Patches measure both the quality and heterogeneity of such areas. In agriculture the aim of a greater crop biomass and reduced heterogeneity leads inevitably to improved habitats for specific pests. This can be redressed, however, if resistant varieties are grown (Section **13.2.4.2**), polycultures are used (Section **13.2.4.4**) and some natural plant communities retained.

12.2.6 The persistence of habitats

So far we have regarded natural habitats as unchanging, which is roughly so relative to the shorter duration of patches and to the life cycles of the insects that live in them. But while rapid seral changes occur on disturbed ground, even climax habitats change in the longterm. This can take a few years to millennia. Rapid change occurs when bracken (*Pteridium*) invades *Calluna* heath, while artificial fertilizers running into it will drive a change to grassland. In disturbed tropical forest another aggressive fern, *Gleichenia,* can become dominant in a few years, greatly altering the habitat. Temperate woodlands can be thousands of years old. Even some herbaceous patches in them are old (Section **12.2.3.1**). Tropical forests are even older, while some individual trees in the *Fitzroyia* forests of Chile (Section **2.2.2.1**) are >3600 years old. Man-modified habitats such as field crops change rapidly, because of harvest, crop rotation or economic dictates, and so in the main differ greatly from conserved natural ecosystems. Orchards, vineyards, banana plantations and olive groves last much longer. But in natural systems, patches are generally located in stable habitats.

As in autecology, the factors that alter natural habitats are physical and biotic, the former generally driving the latter. Long-term climatic changes ultimately depend on plate tectonics, the dynamics of the Earth and Sun (Section **2.2.2**) and bombardment of our biosphere by meteorites. Recently there are tangible effects of global warming (Parmesan, 2006). Atypically, a biotic influence, the expansion of the human population, has likely driven this physical change, the build-up of carbon dioxide, on which plants are feasting. Global temperature changes from whatever cause produce concomitant variations in sea level, which affect coastal habitats especially. In the shorter term and smaller scale there are habitat changes due to fire, flooding, drought, hurricanes and landslides. These set in train seral changes typical of the locality, often in the sequence:

Ruderals → Grasses → Perennial Herbs → Trees and shrubs

each with its own specific insect fauna (Brown, 1985). Then, biotic factors such as human impacts, grazing by herbivores and minor disturbances of gap phases in climax woodlands also cause change. On the time scale of human life such events are infrequent, on the scale of evolutionary history they occur constantly. Globally, forests have been cut down, diminishing from >70% of the land area in 10,000 years before present to <20% in 1999 (Polis, 1999). Marshlands were drained for agricultural expansion (Section **2.2.1**), another factor, perhaps, leading to global warming. Human interference often makes natural habitats smaller and more fragmented, reducing the persistence of their insect populations (den Boer, 1968; Hanski, 1998a). But *regional* increase in crop area leads to higher densities of the pests it harbours (Howard, 1931). For example, in Canada increased growing of oilseed rape has led to widespread, injurious attacks from *Delia radicum* (Section **3.2.2.1(i)**; Soroka *et al*., 2004, in Andreassen *et al*., 2010). In Europe too, increased rape cultivation has led to much higher densities of the pollen beetle *Meligethes aeneus* (Thies *et al*., 2003; Section **6.2.1.2(a)**). It is against this background of patch and habitat lability that we now consider the dynamics of insect numbers.

12.3 Process: The Dynamics of Insect Numbers

12.3.1 General introduction

Having analysed the *spatio-temporal structure* and lability of the insect's world, we consider here the *dynamics of insect numbers* at increasing spatial scales: patch, habitat, landscape and globally. Population *persistence* is directly related to this scale (Richards, 1961; Harrison, 1989; Hanski, 1998b), while models suggest that the *rate of change* of population numbers should become less with this trend (Hanski and Gyllenberg, 1993). Patch dynamics should show the closest fit to those in equations modelling the regulation of numbers (Section **11.5.2**). While at all levels dynamics involve strictly *time-dependent processes*, their outcome, commonness or rarity, or pest status is largely *time independent*. But in *closed systems* the mean density of a species over time, be this high or low, fluctuates around the level at which births equal deaths. As noted in Section **11.4.1**, it may be possible to separate '*harsh season dynamics*' from '*kind season dynamics*', as in Andrewartha and Birch's theory (Section **11.2.2.3**), so giving greater insight.

The main points are:

1. Global dynamics of a species are related to the total spatio-temporal structure of its environment (Freeman 1976, 1981a; Drake *et al*., 1995; Gripenberg and Roslin, 2007). Extending Southwood's (1977) reasoning we consider an *environmental template* (Section **9.2**) interacting with a *global population* (Section **12.2.1**).
2. Global numbers of species vary (Section **9.2**) with their *ecological efficiency* in relation to changes in area and quality of this template. Density must be related *to the spatial scale on which it is estimated* (Section **9.3**).
3. Insects multiply *only by reproduction in patches*, whether these are embedded in habitats or landscapes. Local numbers increase by immigration, but no immigration into global populations exists.
4. For large *populations* (thousands), numbers fluctuate about a mean (Nicholson, 1958; Maynard Smith, 1983b; Section **11.3**), or rarely exceed a ceiling density (Dempster, 1983; Hanski *et al*., 1996). For *population units* (smaller) this is less obvious, extinction common and inversely related to unit size (Hastings and Wolin, 1989), a basic metapopulation concept (Hanski, 1998b).
5. In *populations* this implies either control or restraint (= limitation) (**11.2.2.1**).
6. *A priori* logic demands such mechanisms to be density dependent (Section **11.2.2.2**), but what happens in nature? They operate on births and deaths, often involve redistribution, are altered by physical factors and overridden by them in extremes.
7. Heterogeneity stabilises numbers (den Boer, 1968, 1998; Levin, 1976).
8. Populations vary *genetically* in time and space under a *mosaic of selective forces*. Phenotypes also change by *inherited environmental effects* (Rossiter, 1996), both current and past conditions being instrumental (Benton *et al*., 2006). Good evidence exists (Section **12.3.4.4(e)**) for a genetic component to commonness and rarity.
9. Most species vary about low mean densities (Section **9.4**). While interesting theoretically, this rarely concerns pests.
10. Pests often emerge when the crops they affect become extensive and/or when alternative food plants are plentiful, suggesting that changes in the environmental template determine local density.

Most cases concern metapopulations comprised of local populations that form a graded series:

1. Those of non-migrants in which emigration and especially immigration play a minor role.
2. Migrant species in which local extinctions and recolonizations often occur. Ephemeral patches also promote this.
3. Those which would go extinct, namely they are sinks (Freeman, 1981a; Pulliam, 1988), but immigration often stops this.
4. Those which fluctuate but persist, migrants reducing the size of the fluctuation (Taylor, 1990).

Models agree that asynchronous fluctuations between local groups promote overall persistence.

The following rationale includes themes from *extrinsic* and *intrinsic theories* and the *bottom-up/top-down debate*: as White, T.R.C. (1978) puts it succinctly: 'limited from below' not 'controlled from above'. But victim density often controls enemy density (Thompson, 1929; Varley, 1941; Myers, 1980), rather than vice versa. Also, we must consider *lateral effects* due to other influences of the web (Polis and Strong, 1996). These may include interspecific competition (Price, P.W., 1997), but *trans-specific mortality* (Section **10.2.3.9**), a more explicit term than 'apparent competition' (Freeman and Parnell, 1973; Freeman, 1977, 1982; Holt and Lawton, 1994; Bonsall and Hassell, 1997), is probably more usual. This is so since enemies are many and often polyphagous (Askew and Shaw, 1986; Cornell and Hawkins, 1995) and *operate over a wide range of victim densities*. Indeed, such mortality is a special case of Milne's imperfect density-dependence (Section **11.2.2.4**).

Theoretical populations show an '*endogenous nucleus*' of dynamical behaviour independent of external physical forces (*exogenous factors*) so long as the latter remain within the favourable range (Section **10.1**; Turchin, 2003). The former, often regarded as aspatial, are the favourite concern of mathematical analysts (Section **11.5**), exogenous factors being modelled as random variables. Lewin (1993) argues that these factors must not be so marginalized, being part and parcel of the ecosystem. Indeed, they often override all other factors (Richards, 1961; Milne, 1962), Nicholson's '*legislative factors*', setting the laws for the biotic games being played being fitting. All animals have physiological and behavioural mechanisms buffering them from the vagaries of the physical environment; but these are developed best in large birds and mammals. So we expect their dynamics to show more independence from physical stresses, although these are still powerful when extreme. While insects have diverse buffering mechanisms, including modification of their immediate environment (Turner, 2000; Danks, 2002), they are more influenced by physical factors than these tetrapods.

While there are many processes common to insect dynamics at all spatial levels, new factors emerge as one goes up the scale, especially the growing influence of redistribution and inimical physical boundaries. For regions, the selective mosaic and so local adaptation may be at work, but this depends critically on the amount and efficiency of migration (Haldane, 1956; Brussard, 1984). In less mobile insects, such adaptation can occur even within patches (Mopper *et al.*, 1995). To survey insect dynamics comprehensively, we start at the patch level and move progressively to the global one.

12.3.2 Population units: Insect numbers within patches

12.3.2.1 General introduction

Several empirical studies relate to single or adjacent persistent patches (type 1), giving much of our data (Varley, 1947; Varley *et al.*, 1973; Hassell *et al.*, 1987; Cornell and Hawkins, 1995). But dynamics within them do not represent those at greater spatial levels because there are patch-specific components. Also in many, but not all, species (Section **12.3.1**), migrants leave to scan the environmental template (Johnson, 1969; Freeman, 1976, 1980; Taylor, 1986; Walter, 2003). Dynamics in one patch are but a small sample of the global one (Brewer and Gaston, 2003; Gripenberg and Roslin, 2007), a sample having zero degrees of freedom, with redistribution usually unassessed or worse, confounded with mortality.

Processes driving numerical change in a population unit (Fig. 12.6) are positive (births and immigration) and negative (deaths, emigration), as packaged in the BIDE model (Section **11.5.3**). No sensible discussion of *real* patch dynamics is possible without estimates of these components. Egg laying and usually redistribution are adult affairs, but deaths affect all stages. While some species are effectively non-migrant and habitat-tenacious (Section **12.3.1**), all species move between patches. Several factors reduce the number of fertile eggs produced and distributed (Leather, 1988) from the maximum potential fecundity. But even if fertility fell drastically, unless it fell to two, the mean for replacement (parthenogenesis excluded), it would still promote increase in the unit's numbers. Of course, all mortality factors reduce the unit's ability to increase, while migration by flight is limited by specific threshold temperatures for take-off (Section **10.2.4.2**). So the terms *positive processes* and *negative factors* used below are more inclusive than *natality* and *mortality*, recalling '*biotic potential*' and '*environmental resistance*' (Chapman, 1928) and the new concept of *ecological efficiency* (Section **9.8**).

Combining births and deaths in a simple positive or negative *rate of increase* r_m, a convenient short hand in models, leaves much unsaid in describing

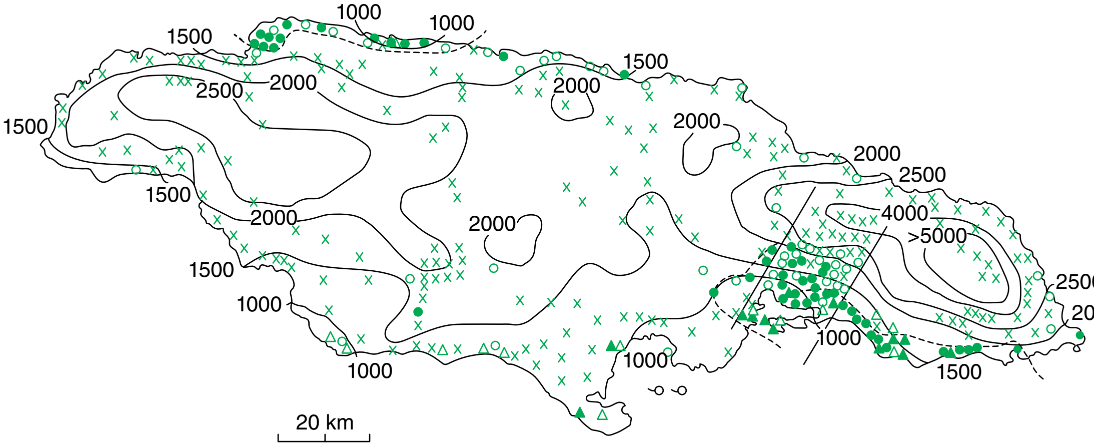


Fig. 12.6. The distribution of *Asphondylia* in Jamaica in relation to rainfall isohyets. From: Freeman and Geoghagen (1989) *Journal of Animal Ecology.* Fig. 1. Reproduced with permission.

nature. The entire picture must be understood before deciding what is to be left out. For physical factors, adverse weather can cause mortality directly, increase the period of development (often leading to a Williams' effect), reduce fertilization, egg maturation and distribution, even prevent oviposition entirely. While it may reduce or abolish parasitism (Messenger, 1964a; Randall, 1982), this is less likely for predation, especially from tetrapods. The components of r_m vary with physical factors, r_m itself being greatest at some *hygrothermal optimum,* although what is optimal for growth is often not so for survival (Section **10.2.3.3**). Thus r_m declines away from these optima, rapidly so near their upper and lower limits. Then, optimal and sub-optimal densities exist for biotic factors (Section **10.2.3.7**). If r_m declines from the best set of factors for our focal species, when these act on its enemies, r_m for our species may increase, two negatives giving a positive. We tease out these factors below, giving an empirical base on which the verity of models can be assessed. Both laboratory studies and field life tables have uncovered many details of within-patch systems (Cornell and Hawkins, 1995).

If physical favourability and patch duration allow, as in patches as large as trees, *Rubus* clumps and clones of perennial herbs, starting numbers often increase for a few generations after colonization ($b > d$), but become progressively restrained by inimical *biotic factors*, until some constancy may be reached. If weather permits, immigration and emigration of both conspecific and other insects, usually as adults, are possible. Immigration levels then depend on the proximity, size, favourability and number of other patch population units within the ambit of redistribution and maybe on matrix connectivity. Emigration levels often depend on patch size, being proportionally greater from small patches. Patches vary in quantity and quality, which together equate with carrying capacity. A balsam fir tree varies in quality for *Choristoneura*. But in crops, patches terminate at harvest and pests are destroyed, emigrate or persist in the soil. Excepting catastrophe (Thomas *et al.*, 1996), such as extensive flooding, the risk of extinction is often inversely dependent on population unit size (Richards, 1961; Freeman, 1977, 1981a; Harrison, 1989; Hanski, 1998a and b). Apart from the open nature of the system, patch dynamics are Milnean. Density dependence may occur even at this small spatial scale (Hanski, 1998b). In adversity positive processes cease, as do some negative ones of biotic origin, such as emigration and mortality from enemy insects. But deaths from harsh physical factors and visiting tetrapods continue unabated or may increase (Fig. 12.6; Section **11.5.2.1**).

12.3.2.2 Positive processes

In *univoltine species* these comprise *production* and *distribution* of fertile eggs laid/year and, in migratory species, on immigration. In *multivoltine species* they also depend on the number of generations/year. Egg production increases under a range of favourable innate and external factors (Sections **10.2.5** and **12.3.2.1**) that operate during juvenile development, ovarian maturation and *egg distribution* (Section **10.2.5.2**). Overall, AF depends on the size and nutritive state of females, but after mating factors donated by males often enhance oogenesis and egg quality (Gillott, 2003), as multiple matings may do (Freeman and Ittyeipe, 1993; Zhou *et al.*, 2015). Apart from the genetic qualities of both sexes, *inherited environmental effects* (Rossiter, 1996; Section **11.2.3**) must be accounted for. So progeny of large *Sceliphron* females survive better since: (i) provisioning cells is faster; and (ii) parasitoids are less able to penetrate the thick cell walls (Freeman, 1981c).

As well as egg production, patch dynamics depend critically on egg distribution, a range of behaviour well shown in the Lepidoptera (Courtney, 1984). Gypsy and bagworm moths dump all the eggs in one batch. Winter moth females are flightless and so lay all the eggs in the *same patch*. When several such females oviposit within a patch, it allows proper assessment of patch dynamics (Varley *et al.*, 1973), although young larvae often emigrate (Wint, 1983; Holliday, 1985). Most small geometrid moths are weak flyers and lay a few egg batches in close proximity, as do burnet moths (Ravenscroft and Young, 1996). Many medium-sized noctuid moths and pierid butterflies lay a few egg batches in several patches, although *Trichoplusia ni* (Section **5.2.1.4(m)**) deposits single eggs on adjacent plants. Large Noctuidae like mullein sharks and most hawk moths exemplify the patchy population model of Harrison (1991). In such HISC species, eggs are placed in ones and twos on small, isolated food plants enough for only a few larvae, not liberally scattered as in swift moths. There is little merit in assessing their dynamics in one patch. They must be sampled widely in the landscape, but a major obstacle apart from finding juveniles(!), is getting a good estimate of AF (Richards, 1961).

Comparing egg numbers in newly emerged females with those left in several old, worn ones is probably as good as it gets and estimates of adult death rates would improve accuracy. Monitoring the fate of juveniles in several patches would allow a life table relating to a habitat or landscape to be made. The progeny deposited by a single female will be subject to a selective mosaic (Section **9.1**). So overall, patch dynamics are influenced by whether adult females are patch residents or vagrants.

The positive processes of reproduction are often discontinuous. In good weather, a population unit starts when females find a patch, lay eggs and stay. The more that colonize, the greater is its genetic diversity and adaptability. If a patch can support several generations (type 1), immigration may continue, especially in *r*-species, increasing numbers, genetic diversity and the capacity for adaptation (Slatkin, 1987; Mopper *et al*., 1995). The potential for increase is normally great. A female laying 100 eggs but leaving only 10 reproducing daughters would produce 1000 great granddaughters were this modest rate to continue (**Eq. 11.1**). Several forest moth populations vary by more than three orders of magnitude, so this scenario is not extreme.

But we must consider immigration further. Such females may on occasion be more fecund than residents, as in *Melitaea cinxia* (Kokko and López-Sepulcre, 2006). We expect most conspecific insects will be from patches in the same habitat. Referring to the central/marginal model (Section **12.1**), in the core of distribution, habitats (and so patches therein) receive migrants from all directions (Gavrilets *et al*., 2000), those near the population edge largely from the core. More generally, what determines the number of immigrants is the proximity, size and favourability (PSF) of *all* inhabited patches, a concept like that in MacArthur and Wilson's (1967) theory of island biogeography. We will term this the PSF concept.

12.3.2.3 Negative factors

Naturally, these are largely the obverse of those above. We consider them here to promote greater insight. By definition any deviation from an optimal environment for a species causes a reduction in its RS. The negative environmental complex reduces and ultimately inhibits AF and can cause mortality to the point of extinction. Mortal risk occurs all the time (**Eq. 11.5**), eggs are laid only under favourable physical conditions, even in species that can breed continuously. Physical factors may be outside the optimum for our focal species, but they can favour or disfavour enemy action (Section **12.3.2.2**). Further biotic interactions, often *between* enemies (Polis and Strong, 1996; Finke and Denno, 2003), also affect mortality in our species.

Complex negative effects of physical factors reduce the size and quality of females and delay egg maturation, should such a period exist. Most females need flight fuel when ovipositing, so bad weather curtails feeding and favourable time for egg distribution. These factors reduce AF, as in a cercopid bug (Whittaker, 1971), in some solitary wasps (Freeman, 1977, 1980, 1981a), the orange tip (Courtney and Duggan, 1983) and a psyllid bug (Hodkinson, 1997). Biotically, mate quality may be critical and, except under parthenogenesis or haplodiploidy, unfertilized eggs are valueless. Lateral effects reducing AF include aggression between ovipositing females, often for limited oviposition sites, as in some butterflies and wasps. Negative bottom-up factors include plant defences (Section **2.4.2**) and scarcity of oviposition sites. When females feed in a patch *during oviposition*, inadequate food further reduces fecundity. This is critical in the success of parasitic wasps employed in biocontrol. Estimated AF in the patch and sex ratio should be added to the life table for the population unit (Varley, 1947; Varley *et al*., 1973; Garraway and Freeman, 1990).

Offspring survival in a patch is reduced *intrinsically* by poor-quality eggs, which often have less yolk, and *extrinsically* by inimical, often top-down factors, the former having genetic and environmental causes. The latter comprise much of life tables (Cornell and Hawkins, 1995). Some extrinsic factors are predictable, others are not. Physical factors may be *unpredictably* severe during sudden harsh weather, as when Colorado beetles and aphids are dashed to the ground by a storm. They are *predictably* inimical during temperate winters and subtropical dry seasons, a regularity driving the evolution of resistant stages. For biotic factors, enemies (Section **8.2.2.2** and **8.2.2.5**) often cause great losses to a population unit. *Resident* enemies may operate as in **Eq. 11.12–11.15**, so their increasing effects are to an extent predictable. *Visiting* enemies cannot be treated like this but can be modelled as a stochastic variable. Their dynamics are determined by factors outside the patch and so decoupled from those of their victims if their local ambit is extensive (Wiens, 1989). Enemies that are *habitat* residents, like anoline lizards, are more likely to stay in a *patch* when the victim's density is high, adding long-term constancy and persistence to its population (below).

The number of enemy species in a habitat is greater in areas *regionally rich* in them (Ricklefs, 1987; Cornell and Lawton, 1992; Caley and Schluter, 1997), which relates to the PSF concept (Section **12.3.2.2**). Habitat richness in enemies can have this effect on patches, as in *Asphondylia boerhaaviae* midges (Section **12.3.4.4(g)**). If the level of numbers to resources is high, competition for them apart from reducing AF, can cause mortality (Milne 1962; Section **11.2.2.4**; and **Eq. 11.4** and **Eq. 11.9–11.11**). In patches (Fig. 12.6) there is field evidence of density independent and directly and inversely density-dependent factors (Freeman and Parnell, 1973; Stiling, 1987; Hassell *et al.*, 1989), the former *all of the time*, the latter pair *some of the time*.

Visiting predators include birds, insectivorous mammals, dragonflies, wasps, predatory flies and spiders (Riechert and Lockley, 1984). They may or may not visit capriciously. Most enemy insects operate only in warmer weather and avian insectivores are more rapacious when feeding chicks. Migrant warblers become ravenous in early summer in temperate regions and in tropical 'winters'. Marquis and Whelan (1994) for Missouri oaks, and Remmel *et al.* (2009) in Estonian boreal forest showed avian predation reduced the numbers of herbivorous insects measurable. But shrews and small myomorph rodents, having high metabolic rates, also require a high-calorie diet and consume large quantities of moth and sawfly pupae in forests (Section **5.2.1.4(g)**), especially in cold weather. Parasitoids arriving from afar usually home in on chemical cues from the plant patch first and from its herbivores second. In *Melittobia*, where most females are migratory (Freeman and Ittyeipe, 1982, 1993), and parasitoids of itinerant hawk moths, such as *Apanteles congregatus* (Braconidae), immigration from the landscape must occur. Using ISC logic, one also expects this to be true of large tachinid flies, such as *Echinomya fera*. Indeed, there is much evidence that flies in the related Calliphoridae move many kilometres (Green and Kane, 1954; Hightower *et al.*, 1965; Bye, personal communication, 2016). On finding the patch, enemies, whether vertebrate or insect, may stay longer and consume or parasitize more victims when these are easily obtained, as in optimal foraging models (Charnov, 1976). Their action may be density dependent, but contains an element of chance, like Milne's imperfectly density-dependent factors (see Fig. 11.10). But on occasion the numbers of a focal, especially *r*-species, increase so fast as to 'run away' from the restraints of all enemies, a process suggested by Howard and Fiske (1911) and embodied in the 'release point' of Southwood and Comins' model (Section **11.2.2.4**).

Enemies of a focal species, having their own enemies be they resident or visitor, add complexity. There are generalist predators (birds, Heteroptera, mantids and spiders), parasitoids, hyperparasitoids and disease organisms (Rosenheim, 1998). These may interact. When the mantis *Tenodera* was added to field plots it caused cursorial spiders to emigrate (Moran *et al.*, 1996). Parts of this web (Polis *et al.*, 1989) reduce the numbers of our species, but others allow it to increase (Snyder and Ives, 2001; Finke and Denno, 2003). And when alternative victims are numerous they may claim the attention of such enemies, relieving pressure on our focal species (Abrams and Matsuda, 1996).

The relative importance of diverse mortality factors in patches has been much debated (Denno *et al.*, 1995; Hunter *et al.*, 1997; Murray, 1999; White, 2001). While the ~30% success rate of biocontrol (Section **13.2.4.6**) argues for the verity of top-down pressures, bottom-up variations in food supply may not appear in crops providing high biomass, throwing enemy impact into focus. Indeed, Hawkins *et al.* (1999) argue that biological control is 'not strictly a "natural" phenomenon'. But the frequent extinction of native non-pest species by introduced biocontrol agents (Howarth, 1991) is evidence of their sustained effect. In many life tables for herbivores mortality from enemies is >60%, as in the spruce budmoth (Morris and Miller, 1954), codling (Clark *et al.*, 1967) and diamond-back moths (Waage, 1983), the sawfly *Pristiphora* (Price and Pschorn-Walcher, 1988) and the leaf miner *Liriomyza* (Freeman and Smith, 1990). Parasitism is often a key factor when such insects are exotic (Hawkins *et al.*, 1999), and high on caterpillars on foliage (Berryman, 1996). Many more cases exist (Cornell and Hawkins, 1995; Hawkins *et al.*, 1997; Tagawa *et al.*, 2008). So today most workers concede roles for top-down and bottom-up processes (Gripenberg and Roslin, 2007).

Good evidence exists in a few species for intraspecific competition. One usually thinks of this 'kicking in' at some high unit density (Milne, 1957a and b; Hassell, 1975; Strong *et al.*, 1984; Murray, 1999; Fig. 12.7). The mirid bug *Leptopterna* (McNeill, 1973) and

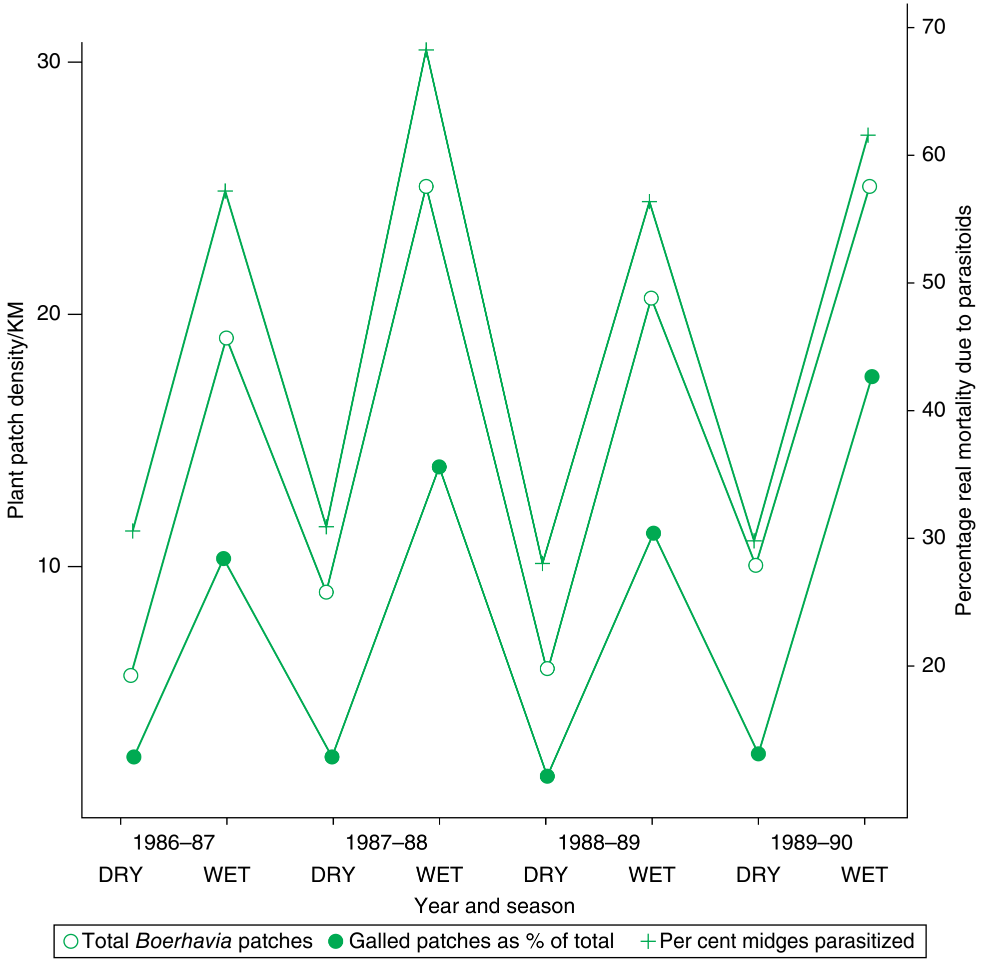


Fig. 12.7. The spatial dynamics of the gall midge *Asphondylia* at Mona, Kingston, Jamaica. The system is driven by seasonal rainfall, which promotes increasing patch size and density of the food plant. This in turn relates to the proportion of plants galled and hence the population density of the midges in the habitat, which then influences the percentage of juveniles killed within the galls by the parasitoid complex.

the moth *Tyria* (Dempster, 1983) provide field examples. But it can occur in a Nicholsonian manner *throughout* the range of density, as in *Euura* (Craig *et al.*, 1990), *Adelges tsugae* (McClure, 1991) and *Melittobia* (Freeman and Ittyeipe, 1993). In the last case, hundreds of larval siblings feed on a host larva (see Fig. 8.14). Within *Asphondylia* galls both intraspecific and interspecific forms occur throughout the parasitoid complex, a veritable blood bath ensuing (Freeman and Geoghagen, 1989). Both types exist in a guild of dung beetles (Giller and Doube, 1989). Interspecific aggression too is recorded (McLain and Shure, 1987). When male *Neacoryphus* (Lygaeidae) try to mate with females of related species, it drives them from their food patch. Even so, Cornell and Hawkins (1995) in an extensive review found a minor role for competition as a cause of mortality. There is much diversity (Murray, 1999).

When patches last for only a single insect generation (Section **12.2.3.2**) or where there are different breeding and refuge habitats, all surviving young adults must migrate, in the latter case twice. The dynamics then comprise reproductive successes and failures of re-colonizing females. Life tables can sample different patches, habitats and generations. When comprehensive they can be summed, giving a cyclic budget (Freeman 1976, 1982; Freeman and Ittyeipe, 1993; Section **11.4.3**) and redistributional losses estimated.

Emigration occurs commonly from persistent patches (Hamilton and May, 1977; Taylor, 1988; Roff, 1994), functioning to spread risk (den Boer, 1998), avoid inbreeding, and competition from kin (Starrfelt and Kokko, 2010), escape enemies or adverse weather. So, season, crowding and reducing patch quality may induce it, or it may have a direct genetic basis (Section **10.2.4.7**). Thus, holocyclic aphids migrate from persistent patches in response to declining food quality, deteriorating physical conditions (Section **5.3.1.2**(**h**)) and reducing photoperiod.

To sum up, numbers in a patch relate to four processes: (i) the patch-specific balance of births and deaths of juveniles and adults; (ii) emigration; (iii) the level of immigration which depends on the ∑PSF; and (iv) chance.

12.3.3 Populations: Insect numbers within habitats

12.3.3.1 General introduction

The dynamics of populations in natural habitats usually involve several population units. So several patches, which may be different (e.g. different plant species) or similar but never exactly the same (Section **12.2.4.3**), must be sampled to estimate births and deaths and build a *habitat picture*, one more complex than that for the patch. Population units are the building blocks of populations in habitats. Winter moths in mixed, broad-leaved woodland are an example, although Varley *et al.* (1973) studied them only on oak. Redistributive losses also occur, either between patches in a habitat (dispersal) or from its periphery (migration; Section **12.3.3.2**). While not all species are migratory, having *fundamentally different dynamics* from migratory ones, in ephemeral patches all adults must disperse in each generation. But several species (*Choristoneura*, *Zeiraphera*), as expected from theoretical analyses (Hamilton and May, 1977; Comins and Noble, 1985), produce compulsive migrants from persistent patches and habitats.

Habitats should be favourable in a general way for a focal species as we assume they have evolved to meet normal physical conditions there, so reducing mortality and dispersive losses. With ephemeral patches populations in habitats are the smallest units of interest, a similar rationale to metapopulations in fragmented habitats or to patches isolated in a landscape. Few dispersive losses during breeding usually occur in crops as such habitats are large and patches contiguous. Since habitat dynamics are intermediate between patch and global dynamics, we use first a *patch-up* perspective and then a *region-down* one, the latter comprising the macroecological influence of immigration (Ricklefs, 1987; Section **12.3.4.4**(**d**)).

In theory, the dynamics of whole populations differ from those in units as density dependence is an unnecessary assumption (Hanski, 1990). In habitats, patches comprise mini-metapopulations with some internal source/sink dynamics. Consider persistent patches of a plant species supporting a monophagous herbivore (see **Fig. 12.4**): (i) the development in different patches may be asynchronous (Hanski, 1991); and (ii) spatial variation will exist especially in the annual variation in number and size of usable patches. Naturally, the dynamics of a polyphagous insect would be more complex. When a female uses several patches in which to lay eggs it should spread risk in space and time and result in longer persistence of the population (den Boer, 1998; Section **9.7**). Of course, no population units persist in ephemeral patches (Beaver, 1979; Shorrocks, 1990). All emerging adults must redistribute. Inter-patch movement and emigration entail losses that may not be sampled, and so be confused with mortality (see **Fig. 12.6**). This relates to the PSF concept (Section **12.3.2.2**) and leads us to examine the role of 'boundedness' of populations and its role in population regulation.

Working from *region down* not all ostensibly suitable habitats are populated by a given species at a given time (Spencer, 1864; Hanski, 1998a), so none of the patches in them will be. While we focus on our given species, because of migration we now wander into the complex maze of synecology, since guilds of mobile species affect it. Physico-chemical factors aside, we must consider the presence, effects and persistence in a habitat of species that have a direct or an indirect action on our species (Thompson, 1929; Hassell *et al.*, 1989; Wootton, 1994). For many of them, however, this action will be small. Many communities are unsaturated with species (Lawton, 1982), and analysis indicates this to be general (Caley and Schluter, 1997), a result following Spencer. So, many species have intermittent interactions with the focal one.

Unsaturated communities arise from past extinctions or mass emigrations from the habitat of species in the regional pool, because *over a long period* all regional species should have found all favourable habitats. While this rationale omits any *new habitats*, extinction and/or emigration, rather than colonization, are key. Of course, some habitats would be only marginally suitable, often due to periodic physical harshness and/or resource scarcity. But mass emigration may take place from perfectly suitable habitats, as in *Choristoneura* (above) and some delphacid pests of rice. In Hertfordshire, UK, in 2008, I found a hawthorn hedge >200 m long swarming with lackey moth larvae, many ready to pupate. In 2009, and to date, none have been found there. Mass emigration is the simplest explanation. Again, some interacting species will be periodic visitors, like migrant birds with uncoupled dynamics, while others will be resident or at least persistent (Section **12.3.2.3**). But what makes a habitat 'suitable' is imponderable, since usually we have no sound ecological knowledge for each regional species. So 'suitability' vaguely describes habitat properties affecting persistence, from optimal to periodically inimical, with sink habitats (Haldane, 1956; Freeman, 1981a) in between.

12.3.3.2 Populations and boundedness

Imagine a population of flightless cockroaches confined to an isolated oasis, a habitat of fixed area, unable to survive in surrounding desert, the bounded population that aspatial models address where numbers and density have an invariant relationship (Section **9.3**). Resources, mainly organic and dead, are limited if not in constant supply. So intraspecific competition for them must ensue unless other forces hold numbers down. This isolate could be *regulated* around an equilibrium level by such competition (Section **9.8**), a bounded Nicholsonian population (BNP), or *limited at a ceiling* by enemies *and* competition (Dempster and Pollard, 1981; Dempster, 1983) as in Milne's theory (bounded Milne population, BMP). The latter, lacking controls at low density, would be less likely to persist if small, fitting observed data well. Some models of such populations predict numbers varying around two or more equilibria according to conditions (Turchin, 2003). If this were the *only population* of our cockroach it would also be its *global population* (see *Papilio machaon*; Section **12.3.4.3**).

In a ~40 ha fen in Berkshire, UK, *Callimorpha dominula* was formerly regarded as such a bounded population (Ford, 1975), as mark/recapture work (Sheppard, 1951) revealed no exchange with a colony ~2 km distant. But while found only in localized habitats, the males in particular are now known to migrate (Goulson and Owen, 1997). *Tipula luna* at Matley in the New Forest, UK, however, *is* restricted to *Alnus* carrs. I collected many thousands of crane flies there in diverse habitats covering many km^2 for 12 years, but no *T. luna* was ever captured away from a carr or its edge. Had they migrated at night then a few specimens would have been found in daytime in other habitats. *Migration must be minimal.* Mark/recapture estimated dispersal between two small colonies *within* a carr of ~1 ha to be only 1.32% (Freeman, 1964). This abundant crane fly exists in many isolated populations in the Forest, as does *Callimorpha* across southern Britain.

But many insects, unlike those above, have unbounded populations (Thompson, 1956; Richards, 1961; den Boer, 1968; Rainey, 1989; Freeman and Ittyeipe, 1993; Hanski, 1998a) with masses of compulsive migrants (Johnson, 1969). *Does this make their dynamics fundamentally different?* Are they not restricted to their migratory arena? But redistribution, particularly migration, involves spatial spread, great adult mortality due to physical causes, and in most cases, no reproduction. Migration produces great loss to the parent population. Locusts breeding in our oasis, like *Locusta* in the flood plains of the Niger (Section **5.2.1.1**(**b**)), would produce emigrants whenever high density was reached. Apart from mortality, density dependent or not, there is *density-dependent emigration* (Nicholson, 1933; Lidicker, 1962; Hanski and Gyllenberg, 1993). Most emigrants die in the desert, the population being unbounded. Later, non-migrants build up numbers as conditions dictate. So long as births exceed deaths within the oasis population it persists. Recall that the survival of large hoppers and the fertility of adults are high, and emigrants would return rarely. Only if a few do so would they have any relevance for our population.

So it does make a difference. Periodic mass emigration into a harsh matrix, where they are unstudied, provides great additional loss. Negative feedback from juvenile mortality, the stuff of classical models, while it may exist is unnecessary for control. Emigration vastly exceeds immigration, the matrix being an absolute sink. Such emigrant populations with overproduction (EPOs), exist in various insects. Barring catastrophes they persist, even if lacking density-dependent mortality and immigration. Apart from wasps (Danks, 1971b; Freeman, 1973a, 1977, 1981a) and bees (Jayasingh and Freeman, 1980; Watmough, 1983; Raw, 1985), EPOs occur in *Conotrachelus* beetles (Mattson, 1980a), the flies *Dacus oleae* (Fletcher, 1987) and *Liriomyza commelinae* (Freeman and Smith, 1990), and *Melittobia* (Freeman and Ittyeipe, 1993).

Eurytides marcellinus (Papilionidae), known since 1725, has a persistent EPO. The core population is at Rozelle in eastern Jamaica. Its larvae feed on *Oxandra* (Annonaceae) in a habitat of a few hectares (Garraway *et al*., 1993b). For several years this population remains sparse and restricted, but irregular outbreaks occur during the May rains. Rapid, low-level, downwind, westward flights of swarms of adults extend >80 km. A few adults may be seen from April to October in other places. Apart from small numbers, its dynamics are like those of *Locusta*. While scattered patches of *Oxandra* exist elsewhere (Adams, 1972), data suggest that only sink units of *Eurytides* exist on them, while the core population being far in the east lacks immigrants. But there is no evidence that another Jamaican swallowtail, *Papilio homerus*, formerly more widespread and known from 1768, now emigrates from either of its two local habitats (Garraway *et al*., 2008).

Such emigrant populations raise the question of fitness. In an EPO we expect strong selection against emigrants if they have lower RS than residents, as seems to be so in *Eurytides*. But non-heritable traits are unselected. In many species every individual has the genetic basis to become either migrant or non-migrant, depending on the conditions experienced during development (Section **10.2.4.8**). Harrison (1980) says '… insects are not, in general, programmed to produce a particular (migratory) morph but are able to respond to environmental cues …'. Such *polyphenism* (Section **1.4.3**), being attuned to extant conditions, must cause fewer losses of maladapted forms than would genetically determined polymorphism (Clark, 1976). But there are many species with mass emigration that fail to establish new populations (Johnson, 1969), as in *Nilaparvata lugens* (Section **5.3.1.2(d)**) into northern Japan (Wada *et al*., 1987) and *Vanessa cardui* from South California towards San Francisco (Abbott, 1951). Amazingly, a low-level swarm of this butterfly was seen 1600 km west of St Helena (Bowden and Johnson, in Pedgley *et al*., 1995) near the mid-South Atlantic. *Pieris brassicae* in Europe generally migrates north in late spring, but the population at Santander on the north coast of Spain heads south east towards Navarra, so not crossing the Bay of Biscay (Spieth and Cordes, 2012). Thus, while such migrations are hazardous, some evidence exists that selection may reduce their risk.

As counter examples, *V. kershawi* in Australia has a return migration (James, 1987) as does *V. atalanta* in Europe (Mikkola, 2003, in Feng *et al*., 2005). In 10 years of trapping four butterflies in Florida, USA, southerly autumn migrations were about tenfold greater numerically than northerly spring ones (Walker, 1991), showing the reproductive advantage of migration. *Nilaparvata lugens* and *Heliothis armigera* in China migrate south in autumn (Riley *et al*., 1991; Feng *et al*., 2005). But the massive spring flights of *Plutella* towards cool temperate regions show little evidence of return. European populations of *Autographa gamma* (Noctuidae) reach Helgoland but die out. Even so, the migrations persist. In some insular Gerridae and Tipulidae, brachyptery has evolved, so selection against emigration *has* occurred. Such cases are more frequent in cold, windy regions (Harrison, 1980; Greenslade, 1983; Roff, 1990), where conditions rarely favour flight. Their populations may thus be bounded, or *viscous*, as in *T. luna*. In all there is considerable variation.

When refuge habitats are sought before a harsh season, a two-way annual migration exists (Johnson's type 3; Section **10.2.4.1**), during which mortality must occur. But how risky would it be to remain were this an option? Logically, migration should occur when its risks, while high, are less than those of staying put (MacArthur, 1972; Baker, 1978). The world of insects is very hazardous. When *Brumus* and *Semiadalia* beetles migrate to the mountains in Kazakhstan and Uzbekistan for refuge, *some* migrants survive but *all* non-migrants die (Yakhontov, 1962). In Jamaica, small, low-density marginal isolates of *Sceliphron,* despite having high levels of breeding success (~89%), vanish periodically, which must be due to *en masse* emigration. These isolates exist in rainy areas that, apart from occasional periods in the dry season, are unsuitable. Using the logic of the cyclic budget (Section **11.4.3**) we see that on average only ~30% of female adult wasps survives to breed (Freeman, 1977). Fitness is maximized by 'the reproductive advantage of a balance between migratory and congregatory behaviours' (Taylor and Taylor, 1977). *Redistribution maximizes fitness*.

In an extensive metapopulation of *Melitaea cinxia* in Finland, extinctions occur every few years in local populations, like another fritillary, *Euphydryas editha* in California (Thomas *et al*. 1996), while 20–40% of adults emigrate (Hanski *et al*., 1998a). In the long term all such groups go extinct (Lawton, 1988). With the exception of successful emigrants, no genes are left to posterity. Extinction results from short-term climatic changes as in El Niño/La Niña oscillations (Cane, 1986) and sun spot cycles (Section **2.2.2.1**). A great catastrophe was the 'super' El Niño event of 600–650 AD in Peru, when ~30 years of heavy rains and then a long drought destroyed the Moche Empire. Eruptions, as at Tambora in 1815, Krakatoa in 1883 and Mt St Helens in 1980, are more recent examples, and may occur at any time (Harrison, 1991; Polis, 1999). Their impact is global, lowering temperatures as megatonnes of ash blast into the atmosphere. Extinction due to biotic drivers also occurs, highlighted when introductions lead to the demise of native organisms (Williamson, 1996).

Although the genetic structure of global populations is considered more fully in Section **12.3.4**, we should be aware of its impact in habitats. A *balance of forces* exists, some promoting uniformity and others opposing it. Mutation and natural selection favour adaptation of local populations and with random genetic drift (RGD) lead to differentiation (Fisher, 1922; Wright, 1931). Migration spreads genetic material and opposes this trend (Mayr, 1963). While the effects of these two forces may be difficult to separate (Hutchison and Templeton, 1999), mass migrants like spruce budmoths have a greater potential for spreading genes and hence maintaining uniformity than sedentary ones such as *Tipula* spp. and *Callimorpha*. Gene flow limits evolution by compromising local adaptation, but promotes it by spreading genes regionally (Haldane, 1956; Slatkin, 1987).

But another view of genetic uniformity over wide areas exists, at least at specific loci (Watt *et al*. 2003; and earlier papers). At the *pgi* locus in *Colias* butterflies (Section **10.2.4.1**) similar ecological forces *in different places* select for the *same genotypes*, so giving uniformity. Watt (2000) warns of the facile acceptance of the RGD paradigm. Even weak selection can override RGD (Ford, 1975). These forces often operate together as in *Callimorpha* (O'Hara, 2005). Then, not all migrants cause gene flow. Even if they survive to enter a new population they may not breed, while their genomes may be like those already in it (Ehrlich and Raven, 1969). These authors and Watt *et al*. note that isolates of some species seem very similar to each other *in the apparent absence* of gene flow, species integrity being maintained (Slatkin, 1985). Also, genetic change has limits (Houle, 1992; Section **9.1**). Indeed, some philosophers of science are critical of the gene flow paradigm (Barker and Wilson, 2010). Again, it is next to impossible to estimate how far migrants travel, as the distribution of displacement has a long positive tail (Taylor, R.A.J., 1978, 1980; Taylor, L.R., personal communication). Recall that a marked *Nilaparvata lugens* in China was found to have flown 720 km (Section **5.3.1.2(d)**), while desert locusts have crossed the Atlantic (Section **5.2.1.1(a)**). Isolated cases indeed, but cautionary ones.

Within habitats, another genetic imperative, *inbreeding depression*, must be considered. When a species like *T. luna* is distributed in small, isolated habitats (Freeman, 1964) there is a greater chance of mating among relatives within each of them. Such assortative mating (Section **9.6**) may lead to inbreeding depression, in which offspring have reduced genetic fitness. This seems to be the case in *Melitaea cinxia* on the Baltic island of Pikku Tytärsaari (Duplouy and Hanski, 2015), a scenario recalling an intrinsic type of population control (Section **11.2.3**). In the long run, however, deleterious genes might be eliminated (Fisher, 1949). But in species with large populations and mate choice, such depression is offset (Mettler *et al*., 1988). Then again, small amounts of inbreeding favour local adaptation (Mopper *et al*., 1995). It is all in the balance.

While migration is risky it improves metapopulation persistence and constancy (Ruxton *et al*., 1997), and may be driven by the greater risk of individuals having unfit offspring. These have, indeed, been found in *Choristoneura* (Rainey, 1989), despite migration, and in an isolate of *Melitaea aurinia* (Ford, 1975; Section **11.2.3**). An EPO is congruent with Thompson's theory: but has a danger zone instead of a sub-optimal zone at the population edge and considers genetic effects. In Thompson's favourable zone, births are greater than deaths, in his harsh zone the opposite is true. Taylor and Taylor's (1977) extensive data show that migrants search the global template for favourable 'holes' where RS is maximized. This is pure Thompson, and shown in the dynamics of *Asphondylia* gall midges (Section **12.3.4.3**).

Sub-optimal zones may act as population sinks (Thompson, 1929; Haldane, 1956; Pulliam, 1988). Data for the metapopulation of *Trypoxylon* in Trinidad (Freeman, 1981a; Section **11.4.3**), with its peripheral sink, strongly supports Thompson's theory.

Risk and reward are the outcomes of emigration, but complexities due to movement within habitats often occur, more so within landscapes. While the use of different patch types is often broadly synchronous, due to the co-ordinating effect of weather, especially in seasonal regions, much variation occurs. Thus, in polyphagous winter moths, while the gross effects of changes of weather influence them on oak and beech in a *similar* way, the microweather within these trees may show significant differences. Beech canopy is denser than that of oak, affecting its microclimate. Winter moths also inhabit orchards, where conditions are rather different, so they are truly landscape species with diverse dynamics (Hunter *et al*., 1991; Roland, 1998; Tikkanen *et al*., 1999, 2000). In bivoltine *Celastrina* butterflies, a *regular* seasonal alternation of patch use exists between holly and ivy (Section **12.2.3.1**). Even desert *Drosophila* are mobile, flying between different necrotic cacti (Johnston and Heed, 1976; Brussard, 1984) probably leading to dynamical diversity and a selective mosaic. In selva, oligophagous insects may move between patches in complex ways, and this requires study. We expect the dynamics in diverse patches in habitats or landscapes to be different and stabilizing in that they promote persistence (den Boer, 1968; Wiens, 1976; Hanski, 1998a). Some pests, such as carrot root and fruit flies, behave similarly, moving between reservoir weeds and crops (Section **13.1.2.2**). *Diatraea* fly opportunistically from old sugar cane to young sorghum and maize. *Heliothis* spp. eat a variety of crops and weeds, and *Anastrepha* and *Dacus* spp. fly between several species of tropical fruits.

12.3.4 Insect numbers: Global dynamics

12.3.4.1 General introduction

These dynamics are the ultimate spatial level, extending the principles for patches, habitats and landscapes. They also embrace the ultimate events of speciation, extinction or persistence. Due to spatial complexity they are difficult to model using the equations in Section **11.5.2**. While *emigration* into extreme areas leads to great losses, the only simplification here is that *immigration* to 'rescue' a species (Gotelli, 1991) is impossible. Global populations are closed to immigration, recalling Turchin's general definition of population (Section **9.5**). While most classic theories (Sections **11.2.2.1** to **11.2.2.3**) outline their dynamics broadly, field data are few due to the extensive area entire species usually occupy. This makes adequate sampling onerous unless trace methods are used (Freeman, 1973a, 1976, 1977, 1981a; Heads and Lawton, 1983; Freeman and Geoghagen, 1989; Freeman and Ittyeipe, 1993; Brewer and Gaston, 2003). Morris and Miller pursued global studies by compiling life tables for spruce budmoths at several sites in Eastern Canada (Morris, 1963). But it is often feasible to estimate only range limits and variation in density, relate them to climatic data, latitude and altitude (Cook, 1924; McDonogh, 1939; Miller, 1966; Taylor, 1986; Section **2.2.2**), make a few local estimates of mortality (Menéndez *et al*., 2008) and perhaps natality. In forest pests (Rainey, 1989; Myers, 1998; Reeve *et al*., 2002) and locusts (Betts, 1976; Cheke and Holt, 1993), the distribution of outbreaks has been recorded.

In such extensive studies we should bear in mind possible regional *genetic differences in our species*, existing in localized but interconnected groups. Since global extinction is rare, how are numbers adjusted between the several populations that normally comprise the global one? This is metapopulation dynamics on the widest scale. Since we must define the area of global distribution we start at its edge and then include the politically popular subject of global warming, largely in relation to the extension of species' ranges in Palaearctic areas. Finally, we consider the great bulk of a species' numbers, those normally contained in the more central core of its distribution (see Fig. 12.4).

12.3.4.2 Range limitation and the population edge

Why does a given species inhabit only so much of the Earth's surface and no more (Section **9.2**)? There is a *global population edge*. Thompson's original, philosophical answer (Section **11.2.2.1**) is that it has 'specific intrinsic limitations' which vary with species. We expect variation but we need definitions and field details. To start, two concentric limits to a global population exist, that to its *breeding range* and that to its *migratory range or area* (Drake *et al*., 1995). In non-migrants these are effectively contiguous. Within the breeding range, however, there are often *sink habitats* (Haldane, 1956; Freeman, 1981a) in which a given species fails to sustain numbers. Populations persist only if immigrants breed there, the *rescue effect*. But if they fail to find the habitat, die during maturation or never mate there can be no rescue. There are *absolute sink habitats* where our species cannot produce viable adult offspring although it attempts to, often because favourable time runs out (Cappuccino and Kareiva, 1985; Bird and Hodkinson, 2005). Several moths from the Mediterranean, such as *Heliothis* and *Plutella*, that migrate to the UK in summer (Pedgley *et al*., 1995; Chapman *et al*., 2002) have offspring that do not survive winter (Sparks *et al*., 2005). The edge of even the breeding range is fuzzy. It ebbs and flows under climatic variation since the area of distribution contracts and expands. So to refine the nature of the '*population edge*', spatio-temporal data are necessary. Finally, there are extensive areas lacking resources in which migrants simply perish, often in great numbers.

Thompson's 'intrinsic limitations of organisms' lacks genetic details, but indeed there may be *genetic limits* to the ability of marginal populations to adapt to worsening conditions (Blows and Hoffmann, 2005; Duplouy and Hanski, 2015). Range expansion could be due to favourable climatic change, to evolution, or both. But many species and groups that are usually confined to warm regions show little ability to expand polewards. In temperate zones some are found in insulated refuges, hospital basements (*Periplaneta*), sewers (*Culex pipiens*) and commercial stores (*Lasioderma*).

Genetics aside, breeding populations are usually bounded globally by an increasingly *harsh climate*, by a *lack of resources* or by some combination of both. We refer here to maintaining a breeding population *locally*, not the regulation of numbers *per se*. Harsh weather can limit resource distribution *and* the searching capacity of our species, but may also reduce the ability of its enemies to find victims, although a new set of enemies may take over from an old set. Since the last glaciation we expect climate to be fully in charge (Coope, 1979), but here we refer to its more subtle changes over the last few decades.

In *climatic limitation* resources are not implicated, harsh climate *acts directly*. While regional and topographical factors drive an increasingly harsh climate for our species, causing a lower birth rate and higher death rate (**Fig. 11.9**), they do not alter *resource density and distribution materially*. Beyond the limit $b = d$, the habitats are sinks ($b < d$), a limit that varies with kind and harsh seasons (Byers, 1961). But in *resource limitation*, often driven ultimately by climate, resources are denser in the core of our species' distribution and sparser peripherally (see **Fig. 12.4**), distance between them gradually increasing (Carter and Prince, 1981). Resource density on a gross scale is less. Local populations using them typically become smaller and more scattered (Freeman, 1977, 1981a; Freeman and Geoghagen, 1989; Brown, J.H. *et al*., 1995; Thomas and Kunin, 1999; Bridle and Vines, 2006). We expect fewer resources to be found by a species near the edge. So range limitation results from resource *scarcity*, finally *resource absence*. Limitation, possibly less often, results from two other biotic effects. First, trans-specific mortality (Section **10.2.3.9**), in addition to other factors, may tip the balance of births and deaths. The verity of this impact is revealed when biocontrol drives non-target species to extinction (Pimentel *et al*., 1984; Lynch *et al*., 2002; Louda *et al*., 2003; Van Lenteren *et al*., 2006; Section **13.2.4.4**). Second, interspecific competition may on occasion cause limitation, but, as in all biotic interactions, the outcome may well be legislated by the physical environment.

For example, several butterflies (*Apatura iris, Limenitis camilla*), are confined to central and southern areas of England (Pollard, 1979; Strong *et al*., 1984; Asher, 2001). But their food plants, *Salix* and *Lonicera,* respectively, are found abundantly far to the north. In Jamaica, the leaf miner *Liriomyza commelinae* is restricted to altitudes <900 m although its water grass food plant extends to 1400 m (Smith, 1987). The northward spread of the butterflies may be limited by cold. Cold and other physical factors act directly or indirectly (Section **10.1**). Thus in summer low temperature might reduce AF and increase the duration of the larval stage *directly*, the latter inducing an *indirect* Williams' effect due to longer avian predation. In winter it might increase larval mortality *directly*. Pollard showed that the range extension >100 years ago of *L. camilla* was mainly to the north, maybe in relation to a warming climate. But parasitism has declined and reduced coppicing improved habitat quality and, in turn, RS.

Thymelicus acteon (Hesperiidae) is confined from at least 1832 (South, 1906) to south-facing habitats in a small region of the south coast of

England. It is at the northern edge of its global distribution (Thomas, 1983). Its food, the grass *Brachypodium pinnatum*, grows only on calcareous soils, but extends farther north and east. Several British Lepidoptera are limited to the south and to the coast. But *Strymonidia pruni* is isolated in a small area of the south-east Midlands (Strong *et al*., 1984), while its food plant, *Prunus spinosa*, is widely distributed. Its restriction may be due to edaphic factors, although this region has a mildly 'continental' climate. Several of these butterflies, while local in the UK, are widespread in Europe. Since they are entirely cut off from the rest of their species we can think of them as *global isolates*.

Masonaphis (Section **12.2.1**) is not limited by its food plant's (*Rubus parviflorus*) distribution, which extends along the Pacific coast into Alaska (55°N) and as far east as the Great Lakes (Gilbert, 1980; Strong *et al*., 1984). This aphid needs several summer generations to complete its full life cycle and cannot do so above ~48°N. In upland Norway, *Craspedolepta subpunctata* and *C. nebulosa* (Psyllidae) have a range of altitude *narrower* than that of their food plant, *Epilobium* (Onagraceae) (Bird and Hodkinson, 2005). The former bug is limited to 988 m, the latter, a blackish species, extends to 1100 m. The authors suggest that the melanic bug absorbs radiant heat better (see Berry and Wilmer, 1986; Section **10.2.2.2**) and so has more time in the short northern summer to complete its life cycle. Here, climate acting directly ostensibly limits distribution. Both species, passing the winter as nymphs on roots, can survive low temperatures. But at higher altitudes *Epilobium* exists only on south-facing slopes, another topographical effect.

While non-resource biotic factors such as enemies often greatly reduce the density of our species (Cornell and Hawkins, 1995), climate limits their distribution and action too, as we have seen. Often, as in aphids and aphidiine wasps in Europe, the parasitoids are more adversely affected by harsh climate than are their hosts (Section **8.2.2.5(m)**). In India, temperatures <20°C favour the aphid *Lipaphis erysimi* while higher ones favour its predator *Coccinella septempunctata* (Atwal and Sethi, 1963). Again, temperature legislates the outcome of competition in two *Nicrophorus* beetles, limiting the distribution of one of them (Wilson *et al*., 1984; above). So climate may affect distribution indirectly.

Asphondylia in Jamaica provides an example of range restriction by *resource limitation*. Its *Boerhavia* food patches become sparser and smaller towards the global population edge, which is often at an altitude of ~900 m. Ultimately, the midge rarely locates them (Freeman and Geoghagen, 1989). But if an isolated plant is found it usually breeds successfully. For *Melitaea cinxia* in Finland, habitat size and spacing affect the chance of occupancy (Hanski, 1998a). *Trypoxylon palliditarse* in Trinidad (Section **12.3.4.4(h)**) is limited at the population edge by resource scarcity (nesting sites) and, due to high rainfall, by having less time to collect larval food. Wasps finding nest sites are less fecund (Freeman, 1981a). In *Ips grandicollis* in Jamaica, climate causes no limitation: the bark beetle is found everywhere its food plants (*Pinus caribea*, *P. patula*) occur (Garraway and Freeman, 1990). But in North America *Dendroctonus ponderosae* is limited by harsh conditions during winter. Its distribution halts at the −40°C isotherm, although the pine trees it inhabits are found much farther to the north and east (Safranyik *et al*., 2010). It is *climatically limited*. One suspects, however, that this contrast is due to tropical versus temperate conditions.

12.3.4.3 The population edge and a warming climate

The above types of range limitation help explain why over the past few decades many Holarctic insects have moved north. It could be due to global warming, so lifting climatic restraint, to a spread of resources, again affected by climate, and perhaps to genetic adaptation? Over past millennia assemblages of beetles have moved in relation to climatic change (Coope, 1977, 1979; Section **8.3.1**); they move rather than adapt. Plants as resources may be similar. But field studies suggest complexity. Genetic changes may have occurred in some north-bound British insects since 1980 (Thomas *et al*., 2001), but are they a cause or a result? The lycaenid butterfly *Aricia agestis* eats new plant species in the area of expansion. But new plants may be added without displacement, as in *Rhagoletis* (Section **6.3.1.1(m)**). Two bush crickets, *Conocephalus discolor* and *Metrioptera roeselii*, have more long-winged forms with better dispersal in the new area (Simmons and Thomas, 2004). Some Odonata (Hickling *et al*., 2005), butterflies (Parmesan *et al*., 1999; Crozier, 2004; Menéndez *et al*., 2008) and leaf miners (Gröbler and Lewis, 2008) are north bound. *Phyllonorycter leucographella*, *P. platani* and *Cameraria ohridella* (Gracillariidae) have colonized Britain from the south east (Grabenweger and Lethmeyer, 1999; Klug *et al*., 2008). The *Phyllonorycter* spp. have moved 8–11 km/a in all directions as a wave, the square root of range with time being linear (Nash *et al*., 1995; Section **5.2.1.4(d)**). Several species have increased their elevational range (Descimon, 2006; Hickling *et al*. 2006). In the tropics this may be their only means of survival (Colwell *et al*., 2008). But an extensive Italian study showed no range expansion of *Culicoides imicola*, a key vector of blue tongue disease (Conte *et al*., 2009).

While some insects have indeed shifted polewards, with climatic or genetic changes as the putative cause, a further cautionary note is appropriate. The paradigm of global warming has led to greater research than formerly, which may bias our data. Parmesan (1996) notes wisely that we need detailed studies to establish the verity of poleward shifts. So, do species expand in other directions? Going back, South (1906) describes changes in the distribution and numbers of several British butterflies in the nineteenth century, at a time when they were collected avidly by a host of informed amateurs, providing much data long before acute global warming and the lavish use of agro-chemicals. Thus, *Polygonia c-album* changed greatly in numbers and distribution. *Papilio machaon*, formerly widely but thinly distributed in south-east England, is now localized in the Fens. *Lycaena dispar* and *Cyaniris semiargus* went extinct. Clearly, *P. machaon*, after many years of isolation in the fens, should be genetically different now from what it was, although this relates to a contracting distribution, not an expanding one. As in *P. homerus* in Jamaica (Garraway *et al*., 2008), it may have evolved to abolish migration. Reduced fitness has occurred in *Melitaea cinxia*, perhaps isolated for a century on the Baltic island of Pikku Tytärsaari. Experiments show that clutch size, hatching rate and spermatophore size there are low. But the moth *Eilema pygmaeola*, recorded by South (1920/1923) as being restricted to a few acres of the Kentish coast, has spread west to Dungeness and north to Cromer. *Phyllonorycter leucographella* (see above) has moved in all directions. While global warming arms us to seek northward movement, we should also seek movement to other cardinal points. Also recall (Section **12.3.4.2**) that many British butterflies are also found across Eurasia; we have dealt only with their global isolates in the UK.

The core of a global population is generally more genetically diverse than at its margins (Wright, 1975; Yamashita and Polis, 1995; Krauss *et al*., 2004; Gaston, 2009b). Marginal isolates, through small size and RGD (Fisher, 1922; Frankham, 1995; Duplouy and Hanski, 2015) may be less capable of adaptation, and inbreeding reduces genetic variance. So we expect they are less able to buffer themselves against the vagaries of the physical environment than are central ones. Even so, specialized adaptations like enhanced cold hardiness are possible. *Drosophila setosimentum* shows great genetic variation in Hawaii at high altitude (Steiner, 1977; Section **10.2.1**), its population edge, where physical factors are harsh and variable. In a *Melitaea cinxia* metapopulation extinction risk relates inversely to heterozygosity (Saccheri *et al*., 1998), affecting larval survival, adult longevity and fertility. So range limits could result from genetic inadequacy, an innate limitation in relation to a harsh environment. But the arrival of any diverse genetic material with immigrants (Brussard, 1984), which is expected in *r* and HISC species, should offset this (Ebert *et al*., 2002).

To expand this theme: forces exist that maintain genetic variation so permitting a positive response to selection (evolvability) (Houle, 1992; Section **9.1**). Immigrants bring genes that can: (i) swamp local adaptation (Haldane, 1956), or (ii) permit better local adaptation (Bridle and Vines, 2006). Models indicate that larger populations utilize genetic variation in changing conditions better than smaller ones (Waxman and Peck, 1999). Further models (Gavrilets *et al*., 2000) employ the axiom that core populations potentially receive immigrants from all directions, peripheral ones mainly from the global core. While not considering genic input specifically, Turelli and Barton (2004) find that genetic variation is diversely conserved (see Hamilton, 1996; Sugg *et al*., 1996; Section **9.1**). Pleiotropic balancing selection and changing allelic effects in space and time can maintain the stable polygenic variation that we often observe. But most of these genetic factors, while applying forcefully to marginal isolates, also apply to any isolate *within the body of distribution*.

Environmental change is often given as *mean* annual temperature, but its extremes are the causal factors (Crozier, 2004). So poleward expansion would be due to less mortality from freezing and/or longer, warmer summers, allowing greater RS. Physical harshness *also curtails migration and so* *colonization*. Such factors are often inimical near the global population edge (Whittaker, 1971; Freeman, 1977, 1981a; Bird and Hodkinson, 2005; Gröbler and Lewis, 2008; Fig. 12.4). While edaphic factors at a place are essentially invariant, *all* physical factors must be studied (Willmer, 1982; Section **10.1.1**). For example, high rainfall in south-west England may prevent *Myzus persicae* from surviving winter, although it is less cold than in their south-eastern retreat (Taylor, 1977). For the moth *Hyphantria cunea* in eastern Canada, Morris (1971) found highest larval densities near the more humid (and less cold) coast. High humidity limits insects directly or legislates a biotic factor. Heavy rain drowns them, but also dashes them to the ground where predation ensues. High humidity allows the spread of fungal disease, as in coastal populations of *Austroicetes* (Section **5.2.1.1(e)**) in South Australia. So biotic effects like increasing pressure from enemies and interspecific competition may be limiting. For example, in two burying beetles (Section **12.3.4.4(h)**), temperature may tip the competitive balance (Wilson *et al*., 1984). The lack of such beetles in tropical lowlands may be due to competition from ants, flies and vertebrate scavengers (Scott, 1998). Despite their applying antibacterial peptides to carcasses (Reavey *et al*., 2014), high temperature gives less time for breeding before the cadaver rots away, a further case of a physical factor affecting competition, here from micro-organisms.

12.3.4.4 Dynamics away from the edge: The big picture

12.3.4.4(a) GENERAL INTRODUCTION. Biogeography, including the distributional history of *single species* (MacArthur, 1972; Coope, 1977, 1979; Cornell and Lawton, 1992), features such as within-species diversity (local races, clines) and more broadly macro-ecology, are ancillary to global population dynamics (Brown, J.H. *et al*., 1995). But a genetic underpinning is an essential. The history of a *faunal* distribution is of less interest for us, except perhaps in relation to regional assemblies of pest species, but that is not our concern here.

In many species migratory capacity, and so *r*-selection or high ISC, is the key attribute in global dynamics. Locusts and diamond-back moths can travel >1000 km in a week, their dynamics are in a grand theatre. See, for example, the scale of work on desert locusts by Betts (1976), reaching from Algeria to Pakistan. Even *Myzus persicae* finds Scotland each summer from its winter retreat in south-east England (Taylor, 1977). Billions of these aphids migrate hundreds of kilometres. So this ambit of movement must be investigated to reveal their overall dynamics, a daunting task, but one foolish to ignore (Freeman, 1976; Taylor, 1986; Rainey, 1989). Dempster and McLean (1998) call for more work on insect mobility relative to population dynamics. Alas, much that is available, such as in the compendious books by Williams (1958), Johnson (1969) and Baker (1978) is often unquoted. Some workers (e.g. Hoffmann and Blows, 1994) lament the absence of existing data. An easy slip to make! Apart from redistribution, recall that insects are constrained by their specific intrinsic limitations (Thompson, 1929, 1956), and in the long term by their patent inability to evolve without restraint (Punnett, 1912; Bradshaw, 1991; Houle, 1992; Blows and Hoffmann, 2005; below). But if a global population is sampled adequately in time and space, a time-independent global life table can encapsulate the result. Strictly such a table, apart from sampling error, refers only to the time period and spatial extent sampled, as Lawton (1988) noted for time series alone. But if ecological conditions change little we can extrapolate so that the table represents a *species-specific characteristic*, indeed a numerical description of its *life-history strategy* (Freeman and Mulder, 2019).

12.3.4.4(b) FURTHER INFLUENCES OF GENETICS. Local adaptation and so genetic differentiation are expected not to develop in strongly migratory insects: they adapt to a *global* rather than a *habitat* template, as in the moths *Triphaena pronuba* (Bishop and Cook, 1975) and *Choristoneura* (Harvey, 1996). Our work is simplified, at least a genetically rather uniform global population exists. But the northward extension of Colorado beetles in Ontario is limited to a few kilometres/annum and gypsy moths are even more restricted. So local races will likely develop. While a landscape picture of the species' dynamics could appear by studying a fairly small area, say <100 km^2, populations elsewhere might well differ in detail, especially because of climatic differences. Thompson's (1929) classic work on European *Ostrinia nubilalis* and that on the leaf miner *Cameraria* (Klug *et al*., 2008; Section **10.2.3.9**) are examples. The sum of landscape pictures gives the global picture with changing suites of parasitoids. Overall dynamical patterns might well be similar, the play familiar but the supporting actors changed.

Although the variability of populations may result from their rapid genetic adaptation to local conditions (Ehrlich *et al.*, 1975; Unruh and Luck, 1987; Mopper *et al.*, 1995; Sections **12.3.3.2** and **12.3.4.3**), we recall that this process may be dismantled with the arrival of genetically diverse immigrants (Haldane, 1956; Slatkin, 1987; Ebert *et al.*, 2002; Bridle *et al.*, 2009). But with modest migration, global populations typically comprise a series of interconnected groups (see Fig. 12.4), those adjacent being more similar genetically than those far apart, as in *Phytomyza ilicis* (Brewer and Gaston, 2003). While the selective mosaic (Section **9.1**) is global, the groups comprising this ensemble are assumed to be interconnected (Hanski, 1998a) and genetically compatible, having not reached the point where hybrids show effective out-breeding depression. We must consider migratory scale (and climatic variation). The several sub-species of *Locusta migratoria*, each separated by thousands of kilometres, provide a classic example of such divergent evolution. *Ostrinia*, a migrant on a lesser scale, forms local races rapidly. Migration and genetic structure are related fundamentally.

12.3.4.4(c) THE INFLUENCE OF MIGRATION. Global dynamics and genetic differentiation greatly depend on the *amount* and *efficiency* of migration. While intermediates exist, such movement, or lack of it, is essentially fourfold: (i) non-migrants; (ii) ground-level migrants traversing the matrix, their efficiency partly dependent on landscape connectivity; (iii) medium-sized moths, speeding along in low-level jet streams; and (iv) small drifting insects wafted high by convection currents. The proportion of insect species that is migratory is conjectural. Data derive from high-level trapping from aircraft (Berland, 1935; Glick, 1939; Freeman, 1945), suction traps (Taylor, 1986), radar scanning (Reynolds *et al.*, 2005, 2008) and ground observations by generations of entomologists. But many small insects, as in group 1, are carried high in the air by accident, not as a regular behavioural phase. Thus, Berland recovered Psocoptera at up to 1000 m and flightless Collembola up to 2000 m.

Group 1 populations inhabit definable habitats in which all births and deaths occur. In habitat-tenacious crane flies like *Tipula luna* and small limoniine species like *Limonia* (Section **12.2.1**) and *Molophilus*, migration is undetectable (Freeman, 1964, 1968; Freeman and Adams, 1972). Taylor (1974) says:

> migration tends to be minimal in the small Nematocera that are behaviourally adapted to fly within a shallow boundary layer at night when atmospheric lift is minimal and, as a consequence, are restricted to travelling short distances their own powers of flight can sustain.

Isolates such as *Callimorpha dominula* (Goulson and Owen, 1997), *Papilio machaon* (Dempster *et al.*, 1976) and *P. homerus* (Garraway *et al.*, 2008) also show evidence of minimal emigration. Several moths, such as *Gortyna borelii* (Noctuidae) confined to two small localities on the south-east coast of England, are similar. It oviposits on perennial grasses near the larval food plant *Peucedanum officinale*, itself restricted to the south east. Dispersal may well be at a slow creep, although occasional violent weather probably transports them, albeit with great loss. *Agonopterix putridella*, which also feeds on this plant, is similarly restricted. Of course, many Orthoptera like some *Scapteriscus* spp., carabid beetles and weevils are flightless and so are essentially non-migratory. If the area they occupy is stable, the classic balance between births and deaths must constitute the major part of their dynamics.

But in migratory species (groups 2 to 4) immigration (I) and emigration (E) become regularly and progressively out of balance ($I < E$ or $I << E$). Their global dynamics are increasingly dominated by losses in the matrix. Low-level migrants (group 2) seek resources with variable efficiency, which is partly related to their size. In landscapes blow flies, many large butterflies and hawk moths (Norris, 1965; Walker, 1991; Hastings and Harrison, 1994) find several food patches. They must suffer less mortality than the group 4 high fliers or their type of egg distribution would be untenable. They counteract vagaries of the wind and have reference to the nature of the ground, so navigating the matrix well. But even in *Sceliphron* (Section **8.2.2.4(m)**), which seeks a complex of nesting resources, only ~30% of females succeed (Freeman, 1976, 1977). Other solitary wasps and bees are similar (Danks, 1971b; Smith, 1979; Freeman, 1981a; Watmough, 1983). Indeed, this may be a relatively high success, and similar to that in bark beetles, like *Phloeosinus*, that employ an assembly pheromone to seek resources efficiently (Garraway and Freeman, 1981). But in the short-lived, delicate gall midge

Asphondylia, success is only 8% overall even though non-migrant morphs exist (Freeman and Geoghagen, 1987, 1989). In life tables for *Ostrinia nubilalis* and some other moths, the greatest mortality results from emigration from the study area (Hudon and LeRoux, 1961; LeRoux *et al*., 1963). Nocturnal mass migrations in the Middle East and North Africa of *Heliothis armigera* (group 3), extend for hundreds of kilometres, as do flights of *Heliothis* spp. in Australia (Fitt, 1989; Feng *et al*., 2005). Success may be 'all or nothing', migrants either find suitable food or they do not. Several culicid and simuliid flies migrate many kilometres (Section **7.3.2.4(c)**), but their attrition is conjectural. We suffer their successes, not their failures. But the great increase in mosquito numbers after extensive rains suggests that this depends on the number, size and proximity of resources in the landscape. In *Melittobia* parasitoids (group 4), <1% of mass migrants find a host (Freeman and Ittyeipe, 1993). Several such *r*-selected pests, for example, aphids (Taylor 1986; Ward *et al*., 1998), frit flies, spruce budmoths (Rainey, 1989) and diamond-back moths (Chapman *et al*., 2002), also suffer great attrition, although aphids at least do not migrate in every generation. Indeed, the basic structure of the global dynamics of these insects has similarities to those of inter-tidal invertebrates with pelagic larvae.

12.3.4.4(d) MACRO-ECOLOGY. Global dynamics needs life tables from representative regions of a species' distribution (Morris, 1963; Whittaker, 1971; Freeman, 1977, 1981a, 1982; Freeman and Ittyeipe, 1993; Randall, 1982; Brewer and Gaston, 2003). But other aspects of wide-scale distribution termed *macro-ecology*, often studied in relation to communities, are relevant. These include the nature, complexity and distribution of inhabited patches and how numerous a species is in local samples. Thus, 'abundant' Hawaiian tree species, namely more 'apparent' patches (Section **2.4.1**) have richer insect faunas than 'scarce' ones (Southwood, 1960), a link found later in other situations, including some insect taxa on British trees. So, are rare plants well defended (*K*-species) and/or are they just hard to find? Both are bottom-up effects, the latter on a landscape scale. Small plants support fewer species than do large ones (Lawton, 1983; Leather, 1986), and in the Rosaceae, trees *accumulate* species faster than do shrubs and herbs (Leather, 1986). Complex plants such as trees often harbour more *parasitoids* than simple plants like grasses. However, koinobionts and idiobionts differ (Hawkins *et al*., 1990). For rock rose, larger patches have a richer fauna than small ones. While inter-patch distance is not a factor (Davis and Jones, 1986), features such as size, patch age, apparency and structural complexity may be at work. We also bear in mind the PSF concept (Section **12.3.2.2**). For cacao and sugar cane, large plantations have more pest species than do small ones (Strong *et al*., 1977). Then, more insect species occur on *widely distributed* plants than on *localized* ones (Lawton and Schroder, 1977; Strong and Levin, 1979), while fleas with the greatest range of hosts have the widest geographical range (Krasnov *et al*., 2005).

For herbivores at least, food diversity affects distribution and dynamics. Polyphagous leafhoppers are associated with unpredictable environments (Novotny, 1994). Polyphagous British moths have less variable numbers than monophagous ones (Watt and Woiwod, 1999). Many noctuid species, whether scarce or abundant, eat a variety of herbs *and* trees, and so are highly polyphagous (South, 1920/1923). Big samples of British and Bohemian moths show direct correlations between numbers caught locally in light traps and (i) variance of numbers in a series of years, and (ii) global range (Gaston, 1988). These links occur in several other groups (Gaston and Lawton, 1988). That of high local density and wide distribution, the *density–distribution relationship* (Hanski, 1982; Hanski and Gyllenberg, 1993), is expected for purely statistical reasons. Abundant species are easily found and several biological causes exist. But in many British butterflies high mobility generally promotes wide distribution and lower local density (Cowley *et al*., 2001). Size is also involved (Gaston and Lawton, 1988). While some large species have restricted distributions and stable numbers, this is usually untrue for locusts and insects with HISC like dragonflies and hawk moths.

Collectively, species generate a range-size distribution (Gaston, 1998, 2009b; Section **9.4**), namely that of the areas occupied by their global populations. This concept helps us relate patch and global dynamics, metapopulation studies being a halfway house. Regional influences on local density are but a subset of large-scale density on small-scale density, not just two-level but multi-level phenomena. Indeed, many pests are widely distributed, often reaching new continents (Section **13.2.4.6**), as have Eurasian forest pests to North America (Niemela and Mattson, 1996). Pests of sugar cane (Strong *et al.*, 1977) and the anopheline vectors of malaria (Section **7.3.2.4**(**d**)), however, while locally dense tend to be regional rather than pan-continental. Recall the strange difference of the pantropical *Aedes aegypti* to the regional *Anopheles pharoensis*. Even so, when *An. gambiae* reached Brazil, it spread rapidly (Section **7.3.2.4**(**d**)).

12.3.4.4(e) TAXONOMIC RELATEDNESS. Closely related species often show contrasts in distribution (Blows and Hoffmann, 2005), which is expected had they speciated allopatrically. But even when sympatric now, they often differ greatly in numbers and density. This may be an outcome of there being 'a selective premium on the [development of] differences' (Mayr, 1948; Section **9.10**) between incipient species, and at root *ecological efficiency* (Section **9.8**). This is *comparative autecology* (Section **9.1**). Apart from *Tipula* (Section **11.2.3**), here are some more cases, mainly from the UK. In *Pilaria* (Limoniinae) the following widespread species are: *P. discicollis* (common), *P. scutellata* (less common), *P. decolor* (rare). *Pilaria meridiana* and *P. fuscipennis* are regional and uncommon. *Plutella xylostella* is a global scourge of brassicas, but several other *Plutella* spp. are regional and sparse (Section **5.2.1.4**(**a**)). In *Ernestia* (Tachinidae), *E. rudis* and *E. radicum* are abundant, *E. caesia* very rare (van Emden, 1954). In Jamaica, the bee *Chalicodoma lanata* is widespread and common, but *C. rufipennis* is sparse and confined to the dry plains (Jayasingh and Freeman, 1980). Many more examples exist, see Section **10.2.3.9** for *Melanoplus*. So the few genes altered in speciation must make great differences to dynamics and distribution. It might just be possible to genetically modify pests to be less ecologically efficient (Section **13.2.4.1**), perhaps using sexual selection. While they are expected to resist, it is a fact the large majority of species are rare (Section **9.4**). The big question is: could we not engineer abundant pest species to be rare? Probably not: the ecologically efficient wild population will always invade. Then, some genera contain many abundant species, others many rare ones, so a *generic* component to abundance and rarity also exists. These relationships have no purely ecological explanation, it must be partly genetic. Of course, the genes involved would be those altered in speciation not those conserved coding for basic physiology and structure (Tautz and Schmid, 1998; Section **9.1**). During speciation genes and genetic variability may have been lost, rendering new species less adaptable, less ecologically efficient overall and so rarer. There is also the possibility of genetic rubbish building up in the genome (Section **9.4**).

12.3.4.4(f) THE OPERATIONAL SEQUENCE OF FACTORS AFFECTING DYNAMICS. Global studies are onerous but informative (Section **12.3.4.1**). Plots of *Austroicetes* numbers and field data for *Asphondylia* midges (see Fig. 11.7) show that *within their area of global distribution,* local climate can determine the extent and level about which numbers fluctuate. Gypsy moths are aggressive forest pests in Eastern Europe but not in more maritime regions of Western Europe. When introduced into England they remained local and rare. Nicholson (Section **11.2.2.2**) appreciated such climatic influences. They are not just edge effects. Even in culture, *Tribolium* numbers vary about levels related to moisture (Holdaway, 1932). Regional climates can be favourable compared to harsh ones elsewhere, as in *Austroicetes*, and weather can be kind or harsh for few or several years, as in *Porosagrotis* (Section **12.3.4.4**(**g**)). In *Choristoneura*, outbreaks follow dry years, locusts and mosquitoes swarm after rains. An *Anopheles arabiensis* plague in Ethiopia (Section **7.3.2.4**(**c**)) followed flooding. There is a sequence of events. Such facts spawned the climatic school (Section **11.2.2.1**) and Andrewartha and Birch's theory of 'kind' and 'harsh' environments (Fig. 11.9). We will first deal with physical factors since they are clearly associated with population levels.

There are two related questions:

1. How are mean numbers, namely a *time-independent* property of a species, determined on local, regional and global scales? This *does not* concern a sequence. In a group of *closely related species* a few are consistently abundant and many always rare (Section **9.4**), so there must be a *genetic component to this relationship* (Section **12.3.4.4**(**e**)). While speciation may be more frequent among rare species (Gavrilets *et al.*, 2000), extending the tail of the SAD, so could be extinction. Abundant species are usually widespread and so adapted to a range of conditions, the *core species* (Hanski, 1982, 1991; Brown, 1984). Satellite species often have small ranges and so adapted to local conditions ('satellite' is something of a misnomer suggesting they are peripheral). But if they are in groups 2 to 4 we expect losses during migration and resource finding to be material although likely to relate to ISC.

2. What *time-dependent processes* control or restrain numbers at these contrasted levels? *This does* concern a sequence. How can extrinsic factors, such as hygrothermal ones varying with region or landscape, *whose action is unrelated to density,* lead to population control *at a particular level*? In Nicholson's view and in many models density dependence is necessary *for control.* As in patches, in extensive populations *proximate physical factors* should, *a priori*, either (i) alter birth rates (*b*) or death rates (*d*) directly (Section **12.3.2**), or (ii) acting as *ultimate physical factors* modify *proximate biotic factors*, which may then regulate or at least limit population.

(1) Proximate physical factors → Alter *b* and/or *d* directly → Change population numbers

(2) Ultimate physical factors → Proximate biotic factors → Population regulation or restraint

System (1) simply leads to numerical change, not to regulation or restraint. Under the vagaries of weather populations could outbreak or dwindle to extinction. But in system (2) physical factors may 'select' a controlling biotic factor, making enemies or pathogens more (or less) effective, forcing victim numbers down or allowing their increase. Only when the physical environment allows (*legislates*) can density dependence operate. The several cases of diminished action by aphidiine parasitoids on their aphid hosts at lower temperature (Sections **5.3.1.2(h)** and **10.2.1**) and the role of humidity on the fungal pathogen of *Austroicetes* provide examples. Such changes in physical factors might well allow control from other causes, perhaps intraspecific competition, at a high density. Equally, higher temperature could have the opposite effect (Burnett, 1949), leading to lower population levels. Control by enemies is 'imperfect' (Milne, 1957a and b) or unreliable. But occasionally a focal species 'escapes', reaching levels at which competition becomes predictably limiting or *en masse* emigration occurs. Of course, physical factors can also affect bottom-up influences, as when drought enhances plant amino-acid levels. This is how physical factors determine mean population levels, or in train, permit their regulation.

While ultimate physical factors are largely hygrothermal, what proximate biotic factors can control or limit numbers and how do they operate? In terms of *trophic levels* are they bottom-up, top-down, lateral, or some combination? Top-down factors, as we saw, are enemies having imperfect control *a la* Milne. Lateral factors (Price, P.W., 1997) are at the same trophic level, but only intraspecific competition, cannibalism and exodus, the last as in our EPOs (Section **12.3.3.2**) can provide perfect control. Like enemies, interspecific competitors have an imperfect action since, apart from the interaction with the focal species, a different complex of factors usually affects their numbers (Milne, 1957a). Bottom-up factors are at a lower trophic level, largely food. So in sequence they affect nutrition, size, egg distribution and so AF.

Biological systems being diverse (Thompson, 1929; Lawton, 1996), we expect complexity not simplicity: Goldberg's lever not Occam's razor (Section **7.3.2.4(d)**). Biotic factors from all levels have complex effects and a *potential* for interaction with the focal species. A food plant may assist a herbivore to resist a parasitoid (Sime, 2002; Section **10.2.3.8**). In different species one or other mechanism may be more effective (Lawton, 1992), although several experienced workers (White, 1993, 2001; Dempster and McLean, 1998; Price and Hunter, 2005) promote the overall significance of bottom-up influence. Some North American forest moth and British butterfly species have clear, cyclic populations that are often regionally synchronous (Pollard, 1991; Pollard and Rothery, 1994; Liebhold *et al.*, 2004; see Cole, 1958, for caveats). Does climate synchronize them (Hanski, 1998b) instead of the intrinsic biotic mechanism often favoured by modellers? But favourable areas vary in size and quality and migration is often a major feature of insect life. So we have:

(3) Regional physical factors → Alter total patch and habitat areas and carrying capacities

(4) Regional biotic factors → Affect resources and migration of a species and its enemies

In system (3) spatial effects are key (Section **11.2.2.1**). Favourable areas within the distribution of a species vary with climate (Section **12.3.4.4(h)**) and weather (Milne, 1957a and b). They act on our species directly, on its enemies, or *alter the carrying capacity of its environment*, usually concurrently. Neither distribution (Taylor, 1986) nor, of course, numbers are constant. So numbers and density, while often correlated, have no constant relationship, the NDA (Section **9.3**). Even so, spatial density dependence may still operate either directly, as in *Sceliphron* (Freeman and

Parnell, 1973) and *Zeta* (Freeman and Taffe, 1974; see Lessells, 1985; Section **11.4.4.2**) or inversely, as in *Trypoxylon* (Freeman, 1981a; Section **12.4**), and the gall wasp *Andricus* (Hails and Crawley, 1992). But in all three solitary wasps the area suitable for breeding is determined by the wet and dry seasons

Just as latitude drives hygrothermal factors globally, invariant landscape and topography alters them regionally. For example, high land has a rain shadow area in its lee (Section **2.2.2.2**). In temperate regions, temperatures decrease sharply with increasing altitude and favourable microclimates are found in fewer and fewer places (Whittaker, 1971, 1985; Randall, 1982). North/south gradients (Harcourt, 1957, 1971; Parmesan *et al.*, 1999; Krauss *et al.*, 2004; Menéndez *et al.*, 2008) and aspect (Thomas, 1983; Weiss *et al.*, 1988; Bird and Hodkinson, 2005) are also important. These features apply, often with less force, in the tropics (Freeman and Jayasingh, 1975b; Freeman, 1977; Freeman and Geoghagen, 1989). Although moving higher has many features in common with moving polewards, incident radiation is unaffected unless greater cloud cover has an effect. In addition, temperature regimes change with distance from the moderating influence of the sea and big lakes (Thomas, 1983; Ravenscroft and Young, 1996).

Apart from spatial effects, hygrothermal factors vary on several time scales. Daytime sunshine and showers may alternate unpredictably, but these factors change more regularly between day and night (see Fig. 10.7). While there are exceptions, for example, the moth *Autographa*, most insects are active either during day or night. Weather varies from day to day, predictably depending on *region*. So while, unlike climate, it is mainly a temporal component of ecology (Section **2.1**), it has spatial aspects. Then there are predictable seasonal and less predictable longer-term variations in climate (Section **2.2.2.1**). Edaphic factors generally have long-term effects except when catastrophic, as in mudslides and earthquakes, although long-term effects ensue. Regional biotic factors are legislated by regional physical factors, just as if each one were itself a focal species. But because work on dynamics has rarely investigated those of enemies, this is often neglected. It follows that an enemy is also a victim; a resource and so a bottom-up influence for its own enemies, like hyperparasitoids. We now examine some classic and some modern global studies and revisit a few equations from Section **11.5**.

12.3.4.4(g) SOME CLASSIC CASE STUDIES ON HERBIVOROUS INSECTS. Most studies on the global distribution and dynamics have been on such insects. Even so, one must often site examples that are not truly global, just widespread. How does the interplay of physical and biotic factors affect distribution and numbers? We start with Cook's (1924) pioneering study of *Porosagrotis* (Section **3.2.1.2(e)**) in relation to climate. While food for this major pest of grain is widespread and ubiquitous, outbreaks to the east of the Rocky Mountains are confined to areas with a moist spring, but low winter and summer precipitation. Mean temperatures vary from −5°C in December to 20°C in July. Heavy summer rain is catastrophic, probably limiting the pest's spread into the Dakotas. Cook mentions 'parasites' once only, without being specific. As in many soil insects (e.g. carabid beetles and elaterid larvae), hygrothermal factors ostensibly affect RS directly. Localized climatic patterns are congruent with those of the cutworm's distribution. Range is limited by climate, not by resources (Section **12.3.4.2**).

Ostrinia nubilalis (Section **4.4.1.1(d)**) in Europe has various physical and biotic restraining factors in different regions (Thompson and Parker, 1928a). In the Rhône basin, persistent north-west winds cause great attrition of young larvae before they enter the plant. The parasitoid complex, with up to ten species, varies in composition with region. Population limitation of this borer is due to a complex of factors: physical, parasitic and agricultural. Importantly, those regions where parasitism is high are not always those where crop damage is low. Borer numbers might well be driving those of parasitoids (section **10.1**). But European *Ostrinia* are not the scourge they can be in North America, again climate may have the upper hand.

Luffia ferchaultella (Psychidae) females are parthenogenetic and flightless. Larvae eat the lichen *Lecanora* on various trees in southern Britain (McDonogh, 1939). Like winter moths, young larvae disperse on silken threads. The 16°C isotherm for July and the 120 m contour largely define its range, but as McDonogh infers, these may relate to exposure and low winter temperature killing the larvae. This rather minor topographical difference limits places where it is found throughout its distribution, not simply at the population edge. *Luffia* is absent from hill tops, from well-shaded woods or trees too far from the woodland edge. This may relate to the mode of larval dispersal. As in

Choristoneura, they require only moderate insolation. Their intensity is also greater near the ground, especially so in the lowest metre (Section **10.1.1**). Food quality and tree species also have effects, the latter relating mostly to the suitability of bark for pupation. McDonogh does not mention parasitoids. Limitation is largely by climate driven by topography.

Whittaker (1971) compared the dynamics of *Neophilaenus lineatus* (Cercopidae) in a 'kind' lowland field with those at ~550 m on 'harsh' moorland in northern England. Up to three batches, totalling 35 eggs, were laid in the field. The population was 'well regulated' by parasitic *Verrallia aucta* (Pipunculidae), which was absent on the moor, where the bug was 'poorly regulated'. Bad weather could delay nymphal growth, stop some adults maturing, or laying even a single egg batch. Higher up they became extinct. On this moor, Randall (1982) described effects of an altitudinal gradient of 15–610 m on dynamics of the moth *Coleophora alticolella*. Food supplies, seeds of *Juncus squarrosus*, diminished at high altitudes because they failed to set. These resources driven by climate limited the moth's distribution. Larval parasitism, mainly from *Elachertus olivaceus* (Eulophidae), also diminished with altitude, parasitoids being absent above 395 m. Physical factors driven by topography restricted enemy influence. Juvenile densities were highest in the 200–400 m band, leading to density-dependent competition for food in a Milnean fashion, to increased mortality in winter and to reduced AF in the next year, another sequential effect.

Aricia agestis (Lycaenidae) has an extensive metapopulation in south-eastern England (Menéndez *et al.*, 2008), feeding mainly on *Helianthemum* (Cistaceae). A former *variety* recorded in Scotland (*artaxerxes*; South, 1906) is now regarded as *A. artaxerxes*. Over the last 40 years, that part of the population moving north is using new plants, *Geranium* and *Erodium* (Geraniaceae), on which larvae develop faster. A warming climate may have allowed this spread, that is, a relaxation of climatic limitation. Northern *A. agestis* suffer less parasitism than in the south, but trans-specific parasitism from braconid wasps occurs via the widely distributed blue *Polyommatus icarus*. Two such wasps, *Cotesia astrarches* and *Hyposoter notatus*, occur in both hosts, the former causing higher levels of parasitism in the north and the latter doing so in the south. Even so, *Aricia* may have partially escaped its parasites by the move, as in system (2) (Section **12.3.4.4(f)**). We need more studies on north/south effects (latitudinal effects) and other physical gradients on global dynamics of contrasted insects, as they give us an increasing insight into the effects of climatic change.

Now for a few cases depending on water and moisture. In the UK, the density of *Tyria* moths within their region of distribution, is determined largely by the biomass (*quantity*) of their ragwort food plant in the habitat, namely *patch density*. This depends on annual rainfall (Dempster and Pollard, 1981). Juvenile development of *Papilio machaon* in England relates to the *quantity and quality* of its marsh food plant *Peucedanum*, which in turn depends mainly on the water table level, and so again on rainfall. Incredibly there are no parasitoids (Dempster *et al.*, 1976). In Japan, flooding after a typhoon promoted the regrowth and quality of the willow food plant of *Plagiodera versicolora* (Chrysomelidae), increasing its density (Nakamura *et al.*, 2005). This occurred despite an increase of its ladybird predator, *Aiolocaria hexaspilota*. For the galling sawfly, *Euura lasiolepis*, rainfall promotes long, fat willow shoots in which mortality is less (Price *et al.*, 1998). Top-down effects are negligible. In all these cases, *the physical factor of precipitation determines the size and quality of the food resource*, which then affects numbers, as in system (2) in Section **12.3.4.4(f)**.

Extensive data on rainfall are available for the dynamics of the gall midge *Asphondylia* in Jamaica (Freeman and Geoghagen, 1989; Freeman, unpublished data; Fig. 12.7; Section **10.2.3.10**). The latter is based on the fate of >100,000 eggs sampled in 825 patches, some several times, for 7 years and about 100 generations. There are two separate populations, the larger in St Andrew/St Thomas in the south east and the smaller in St James and Trelawney in the north west. The midges are mostly limited within the 1500 mm mean annual precipitation (MAP) isohyet, but in St Andrew they tolerate a bit more rain. The food plant, *Boerhavia diffusa*, is found where rainfall reaches 2000 mm MAP, but plants are rarely galled near the population edge. Within these main areas, variation in *seasonal rainfall* determines the number and size of the food patches (Table 12.1). There is an annual fluctuation in the *carrying capacity of the landscape*. In the dry season (December–May) patches become smaller (mean 0.50 m^2 versus 0.76 m^2 in area) and more scattered (mean 2.38/km versus

Table 12.1. Estimates of spatial parameters in two seasons with 95% c.l. for *Asphondylia boerhaaviae* gall midges in two landscapes combined of *Boerhavia* patches, St Andrew/St Thomas and St James/ Trelawney, Jamaica. Data are from 1986–1990.

Season	Patches sampled	Patch area (m^2)	Patches/km Total	Patches/km Galled	Mean densities of galls per m	Mean densities of galls per m^2
Wet						
1986	46	0.85 ± 0.18	1.95	0.99	96.1 ± 16.5	235 ± 45
1987	140	0.79 ± 0.12	2.73	1.54	73.9 ± 6.3	459 ± 63
1988	42	0.80 ± 0.20	2.18	1.01	90.9 ± 21.2	341 ± 77
1989	89	0.74 ± 0.16	2.58	1.63	78.7 ± 10.5	412 ± 68
1990	43	0.61 ± 0.17	2.44	1.86	70.2 ± 10.0	436 ± 79
Dry						
1987	46	0.46 ± 0.11	0.67	0.17	95.7 ± 17.7	536 ± 108
1988	73	0.41 ± 0.07	0.90	0.22	99.1 ± 13.7	534 ± 94
1989	26	0.56 ± 0.16	0.52	0.09	70.1 ± 16.3	362 ± 84
1990	92	0.56 ± 0.14	0.92	0.20	80.6 ± 10.7	658 ± 119

0.75/km apart) and the midge finds less of them (22% versus 58%) than in the wet season (May–December). There are several generations *in each season*. Its dynamics cannot be unravelled unless these seasonal differences are appreciated. Even so AF, at ~100 eggs/female, the mean density of galls/m of stem and the density of galls/m^2 of patch show little seasonal variation. Emergence in the wet season averages only 11.2%, but 41.7% in the dry season (Table 12.2), when smaller patches tend to have high emergence levels (Table 12.3). This may relate to their having fewer parasitoids (*Calorileya*, *Eurytoma*, *Heterolaccus, Torymus*). Indeed, most of the expected density relationships operate at this time, when patches are small and scattered, but not in the wet season when they are large and close. Then the link between patch size and the *number* of enemy species, the latter correlating with the midge's breeding success, is often significant in the dry season, but with one exception not in the wet season, a result one could not anticipate. These relationships must buffer the midge against extinction on a landscape scale in the dry season.

Asphondylia's dynamics provide insights into those of mosquitoes (difficult to study in the field, but also Nematocera), driven by rainfall in the seasonal tropics (see above and Section **7.3.2.4**(**d**)). In both cases the density of breeding sites and thus insects in the landscape are greater after rain. In the midge, density is low in the dry season but its breeding success is higher. Does this occur in mosquitoes? At this time we assume that dispersive losses in both groups, in relation to the scarcity of resources, is greater. *Asphondylia* lacks diapause, a prominent feature of many culicine mosquito eggs. Mosquitoes have no parasitoids (Section **7.3.2.4**(**c**)), but in *Aedes* at least intraspecific competition in patches is common (Juliano, 1998). Without spatial data the relationship between high RS and low density in the midge is a paradox, although congruent with Nicholson's theory. Such bottom-up drivers of density also occur in bark beetles that attack moribund trees. The number and density of such trees determines the numbers of beetles in forest landscapes (Raffa and Berryman, 1987). Density dependence in *Asphondylia* is on a *landscape* scale, there is no such relationship to patch size or to midge density within patches. Numbers are 'squeezed' from top and bottom. Namely, *top-down* and *bottom-up* factors operate hierarchically (Moreau *et al*., 2006; Gripenberg and Roslin, 2007). So we can regard a physical factor, through the victim's supply of food, as determining the mean numbers of both victim and enemy, as in Nakamura's beetles:

Physical factor → Biomass of plant food →
Numbers of herbivore → Numbers of enemy

Whereas a more traditional approach is:

Physical factor → Biomass of plant food →
Numbers of herbivore ← Numbers of enemy

These sequences recall that of the distribution and density of *Austroicetes* (Section **5.2.1.1**(**e**)). It is limited by rainfall in two directions, excessive dryness

Table 12.2. Dynamics of *Asphondylia* in *Boerhavia* patches in two Jamaican landscapes according to season.

Season	Patches sampled	Mean fecundity	% Emergence of adults	% Parasitism of juveniles	Mean number of enemies/patch
Wet					
1982	46	*	19.28 ± 5.39	61.99 ± 5.48	3.80 ± 0.37
1986	46	98.2 ± 20.4	11.78 ± 3.86	54.09 ± 5.12	4.04 ± 0.37
1987	140	91.4 ± 19.1	8.69 ± 2.38	61.07 ± 3.04	4.11 ± 0.20
1988	42	86.3 ± 17.8	15.67 ± 6.89	56.76 ± 6.99	3.63 ± 0.35
1989	89	95.6 ± 15.7	8.01 ± 2.54	59.99 ± 4.89	3.90 ± 0.28
1990	43	99.4 ± 21.6	16.10 ± 4.89	46.56 ± 6.56	3.91 ± 0.36
Dry					
1982	17	*	54.33 ± 13.37	23.00 ± 12.37	1.94 ± 0.59
1983	35	*	45.73 ± 10.31	35.03 ± 9.03	2.79 ± 0.59
1987	47	97.3 ± 21.5	43.24 ± 8.86	24.19 ± 7.04	2.27 ± 0.46
1988	73	102.7 ± 18.2	44.18 ± 6.72	29.75 ± 5.51	2.67 ± 0.35
1989	26	103.1 ± 38.1	39.13 ± 10.42	27.60 ± 9.00	3.12 ± 0.64
1990	92	101.1 ± 22.2	40.39 ± 6.05	31.83 ± 4.91	3.00 ± 0.30

There are approximately ten generations of the midge during each wet season (May–December) and seven generations during each dry season (December–May). The sample means, which are based on the fate of a total of >100,000 eggs in the field, are given with 95% confidence limits. Data for 1982–1983 are based on dissections made by Andrea Geoghagen, the remainder on those of the present author.

*, No data.

Table 12.3. Dynamics of *Asphondylia* in *Boerhavia* patches in two Jamaican landscapes. Spearman's non-parametric correlation coefficients (rho) are given; probabilities are in brackets.

Season	Patches sampled	Patch area (m^2) vs % emergence	Patch area (m^2) vs number of enemy species	Number of enemy species vs % emergence
Wet				
1982	46	*	*	−0.212 (ns)
1986	46	−0.075 (ns)	+0.023 (ns)	−0.220 (ns)
1987		−0.156 (ns, 0.065)	+0.051 (ns)	+0.036 ,(ns)
1988	4	+0.142 (ns)	+0.268 (ns)	+0.065 (ns)
1989	89	+0.063 (ns)	+0.378 (<0.001)	+0.003 (ns)
1990	43	−0.055 (ns)	+0.179 (ns)	+0.088 (ns)
Dry				
1982	17	*	*	−0.605 (=0.01)
1983	35	*	*	−0.581 (<0.001)
1987	47	−0.417 (0.004)	+0.236 (0.096, ns)	−0.553 (<0.001)
1988	73	−0.240 (0.040)	+0.361 (0.002)	−0.636 (<0.001)
1989	26	−0.346 (ns)	+0.580 (0.002)	−0.694 (<0.001)
1990	92	−0.352 (0.001)	+0.388 (0.001)	−0.321 (=0.002)

*, No spatial data are available for these years.

or excessive wetness on a north/south regional gradient. The former results in poor food for young nymphs, a climatic effect on a resource (bottom-up), the latter promoting fungal disease, a climatic effect on a pathogen (top-down). North/south effects also occur in diamond-back moth ecology, Colorado beetles (Harcourt, 1957, 1971) and doubtless many other species.

12.3.4.4(h) GLOBAL DYNAMICS OF INSECTS OTHER THAN HERBIVORES. So far we have considered only herbivores. But we need to understand the distribution and dynamics of predatory and parasitic insects too, and for completeness also those of detritivores. While there are several studies of parasitoids in culture, fecundity aside, this tells us little of their natural dynamics. The better-known although still limited field data are for predatory insects. First, the *distribution* of some solitary wasps. In Jamaica, altitude and rainfall are positively correlated in most areas: topography legislates. In turn the number and *suitability* of nesting sites for these beasts (Section **8.2.2.4(n)**) diminish at higher elevations. Food, judged by the rapid rate at which they collect it (Freeman and Johnston, 1978a; Taffe, 1983), is plentiful. *Sceliphron assimile* is confined to areas <300 m altitude and <3000 mm MAP (Freeman, 1977), *Trypoxylon texense* <300 m and <2000 mm MAP (Jayasingh and Freeman, 1980a), *Pachodynerus nasidens* <400 m and <2400 mm MAP (Freeman and Jayasingh, 1975b) and *Zeta abdominale* to <600 m and <1905 mm MAP (Freeman and Taffe, 1974). But the pompilid wasp *Auplopus bellus* nests at up to 1540 m, where the MAP is >3000 mm. The distribution of solitary bees is similar (Raw, 1985). Flight in these aculeates is apparently unaffected by altitude itself and females select suitable places to nest, resulting in low juvenile mortality. For *T. palliditarse* in Trinidad the quality of the nesting resource, the microtopography of inclined rock faces, gradually deteriorates with higher rainfall and increasing habitat wetness (Freeman 1981a; Section **11.4.3**). Suitable, permanently dry surfaces become few (as do sites for Hodkinson's bugs, above).

In Jamaica, wasp AF varies between ~9–15 in most species, rather less in the rare *Monobia mochii*, but unlike *nesting frequency,* is unrelated to altitude. In *Sceliphron* at least, juvenile survival is ~80% near the population edge falling to ~45% in the lowlands at high density. This is due largely to spatial density dependence from *Melittobia* (Freeman, 1977). But births exceed deaths everywhere. In Trinidad, mean AF for *T. palliditarse* falls from ~12 to ~7 in montane valleys, probably due to a shortage of nesting time because of rain. But there is a big increase in deaths from parasitoids, juvenile mortality rising from <10% to >80%. These valleys are population sinks (Freeman, 1981a). Confounding limitation by wetness with that by temperature in the tropics is unlikely. During the day the latter is rarely <25°C. Topography drives physical factors that limit wasp distribution. For behavioural aspects of these dynamics see Section **12.4**.

For carabid beetles at Kralo Heath, a diverse area of ~6 km^2 in the Netherlands, there are spatio-temporal data from 1959–1985 for *Pterostichus versicolor, P. lepidus, P. diligens, Amara lunicollis* and *Calathus melanocephalus* (den Boer, 1998), an outstanding study in comparative ecology. The numbers recorded each year are the annual catches in pitfall traps, each species being sampled at several sites. The numbers of most species vary by less than two orders of magnitude, some even less, but in *C. melanocephalus,* a small species, they vary rather more. Numbers at these sites vary synchronously (see Fig. 3.10 in den Boer, 1998), especially when close together, less so when as far apart as 2 km. In *P. versicolor*, however, synchrony is less apparent (see Fig. 3.6 in den Boer, 1998). Egg mortality, largely from nematodes, is high in both species (van Dijk and den Boer, 1992). In the laboratory, conditions as mild as 5°C for *C. melanocephalus* and even 12°C for *P. versicolor* result in high death rates. In the field excessive wetness during winter is inimical. Inefficient predation is a consistent feature of all feeding stages, in contrast to that of the solitary wasps noted in Section **10.2.3.9** and above, another example of the profound contrasts between insect orders, one in which ISC is often explanatory. Also recall that the distribution and efficiency of attack by two enemies of *Icerya purchasi* (Section **4.3.5**) in California, *Rodolia cardinalis* and *Cryptochaetum iceryae*, are influenced by environmental aridity.

Very few data exist for field populations of parasitoids (Section **11.4.4.1**), globally or otherwise. While data for temperate *Cyzenis albicans* and *Bessa harveyi* (Tachinidae) are limited, their numbers may be strongly impacted by physical factors. By contrast, the ectoparasitoid *Melittobia* (Section **8.2.2.5(p)**) in Jamaica, unlike its host wasps (above), seems uninfluenced by such factors. But its dynamics are biotically complex since it afflicts three aculeate groups (Sphecidae, Eumenidae, Megachilidae) (Freeman and Ittyeipe, 1993), whose various distributions are determined by altitude (above). AF within host cells varies with host size, from 86 ± 45 on the little bee *Megachile* to 606 ± 102, 95% confidence interval on the large wasp *Zeta*. These wide limits result because *intraspecific* variation of host size also influences *Melittobia*'s fecundity. Correcting for superparasitism, estimated mean AF is 289. As juvenile mortality is only ~25% and 93–96% of the progeny are female, a huge excess of female offspring remains. Other parasitoids on these hosts, the satellite fly *Amobia* and the cuckoo wasp *Hexachrysis*, have no restraint on *Melittobia* since it promptly parasitizes them too. Indeed, they may promote its *increase*. Global numbers are limited by massive losses during migration when hosts are scarce. But its parasitism on *Sceliphron* in north-west Jamaica is higher than that elsewhere (Freeman, 1974, 1977), possibly due to trade winds blowing the little migrant parasitoids in that direction.

A case of physical and biotic factors acting sequentially concerns a detritivore of vertebrate remains (Wilson *et al*., 1984). Using >1000 dead mice they studied the effect of temperature on interspecific competition in two *Nicrophorus* burying beetles (Section **10.1.2**) in Michigan, USA. Most mice were found quickly (24 hours), but *N. orbicollis* displaced *N. defodiens* at higher temperatures. The former species does best from June until August, the latter does better before and after this period. Adult size within and between species was also a factor, larger individuals being more competitive. So competition modulated by temperature limited the southerly extension of *N. defodiens*. Again, a physical factor was the ultimate driver.

These examples clearly show how the living world is driven by the physical one, which then affects more proximate, often regulatory biological responses. In turn, the gross supply, density and distribution of resources often determine numbers at the *habitat and landscape levels*: increase the number of suitable patches and population size increases. Landscape populations depend on the density and favourability of habitats. But if we study the dynamics of only a single patch this effect eludes us. Recall the example (Section **9.3**) of the density of cabbages in a 1 ha plot on the numbers of *Brevicoryne:* more cabbages more aphids. This affect was recognized by Nicholson (1933) and recently found in German populations of the lycaenid butterfly *Polytommatus coridon* (Krauss *et al*., 2004). Apart from the increased mosquito numbers at the landscape level after rains (Sections **12.3.4.4(c)**, **12.3.4.4(f)** and **12.3.4.4(g)**), when the landscape area of an agricultural crop increases, so does the severity of pest attack. The midge *Dasineura* provides two examples: *D. brassicae* on rapeseed and *D. oxycoccana* on blueberries (Section **6.2.1.2(k)**). Then, more migrants will arrive at every suitable habitat and patch. But to unravel such an effect, precise definitions of insect numbers and densities (Section **9.3**) of the spatial levels they occupy (Section **12.2**) and of their redistributive capabilities (Section **10.2.4.1**) are essential. Remarkably, Verhulst's logistic still has currency (Berryman, 2003), but only if the levels of resource space are defined and variation in them taken into account.

12.4 Evolutionary Themes in Insect Population Dynamics

Different species and their populations have different dynamics (Lawton, 1992), who says, however, '… there is a multitude of essentially trivial variations on a few common themes. How few remains to be seen, but it is not many'. That is comforting, but what dynamics are we talking about? What might be the common 'themes' and the rules for defining them? We might fairly ask if insect dynamics, and by extension their LHS, have evolved with their phylogenetic advance and so taxonomy (Price, 1997; Dempster and McLean, 1998). In the beginning, evolution of flight allowed insect populations unprecedented mobility, usually uncoupling adult dynamics from those of their juveniles (Section **9.1**). But we expect their dynamics as a whole, to have evolved as a result of increasingly efficient flight, enhanced ability to seek, find and use resources and better avoidance of enemies. We might also expect such advanced insects to be the most abundant insects. But this is not so. From the Jurassic at least (Section **8.2.2.1**), many enemies of herbivores are insects co-evolving with them, limiting their numbers. Co-evolution with food, mainly against the defences of living plants (Section **2.4.2**) (Southwood, 1985) must also have been a factor, especially in relation to the increasing complexity of the mouthparts (Labandeira and Sepkoski, 1993). But no animal group evolves as a unit. As in the development of zygomorphic flowers in Angiosperms, they evolve along several distinct clades. Because insect orders separated from early times the evolutionary advance of their dynamics must have been along parallel lines. Apterygotes have never made much impact except in cryptic environments (Section **9.4**), nor do they ravage plants. And in exopterygotes only the Anisoptera has moved far along the ISC path. But in endopterygotes several families in three of the four largest orders, Lepidoptera, Diptera and Hymenoptera, have achieved this route, a development we expect to have impacted their dynamics.

Even within groups as small as genera abundant and scarce species exist (Section **12.3.4.4(e)**). A large genus may have its own, typical J-shaped SAD (Section **9.4**). Many taxa with species having dense populations are not advanced (Section **12.3.4.4(e)**).

As above, most Apterygota have cryptic lifestyles, but Collembola (Section **8.2.4**) at least, while poorly represented in exposed situations, are numerous in the soil reaching 10 million/ha. On plants they often graze the *microflora* on leaves and branches (Turner, 1983) rather than chew leaves directly. Numerical success is not the same thing as evolutionary sophistication. As in birds and mammals, evolution in pterygotes has shown another general feature, greater independence from physical restraint (Section **9.2**). Again, we must distinguish abundant species from groups with numerous species (Section **9.4**). No apterygote order has many species, nor do the primitive exopterygote orders such as the Plecoptera, Ephemeroptera and Zoraptera (Richards and Davies, 1988). Phylogenetic advance favours colonization of harsher, variable, plant micro-environments which promote speciation within them (Mitter *et al*., 1991).

A further evolutionary trend in insect dynamics centres on adult behaviour. In the beginning, mass exodus flights were probably associated with mating, an activity seen today in mayflies along rivers and in termite reproductives after rain. No localized resources are sort directly, re-distribution results from the needs of out-crossing and mate finding. Mortality may be high (Borror *et al*., 1989). But with advances in flight capability, exodus after mating becomes distinct from resource seeking (Johnson, 1969; Zera and Denno, 1997). Extensive resources like phytodetritus require less ISC than localized ones such as individual flowers and insect victims, a trend seen in hymenopteran evolution (Malyshev, 1968; Gauld and Bolton, 1991). But not all species are migratory. And in ecology we must consider environmental evolution too. With the advent of flowering plants (Bennettitales 225 million years ago, Angiosperms 135 million years ago; Section **8.2.1.1**) such resources became more patchy (see Janzen, 1981) and more complex, requiring efficient searching. There are two distinct modes. First, *en masse* scanning by huge numbers of small, inefficient offspring, incurring great mortality (Taylor, 1984; Ward *et al*., 1998). Here *r*-selection may have overridden that for large size and ISC. Second, small numbers of relatively large efficient seekers (Freeman, 1977, 1982). Patterns of births and deaths can be very different in each case, while developments in the second mode lead to diverse outcomes (see below).

From field data, I suggest the following conceptual layers of population processes:

1. *Time-dependent* dynamics proceed at patch, habitat and global levels that form the environmental template.

2. Insects are either non-migratory (Section **12.3.4.4(c)**), or perhaps more often, migratory using diverse flight mechanisms (Brodsky, 1994). In *habitats* the densities of the former are determined in the classic manner only by births and deaths.

3. Ratios of births to *juvenile deaths*, namely developmental mortality, fall into four *time-independent* groups, Lawton's 'themes' perhaps or 'first-order' processes regarded as LHSs: (i) high fecundity, high mortality species (*Aphis*, *Cyzenis*, *Tipula* and probably *Manduca*); (ii) low fecundity, low mortality species (*Sceliphron*, *Zeta* and maybe beetles with parental care (Klemperer, 1983a; Heg and Rasa, 2004)); (iii) high fecundity, low mortality species (*Conophthorus*, *Dacus oleae, Melittobia,* and probably *Chrysonotomyia* (Section **11.4.3**)); and (iv) low fecundity/high mortality species, which cannot persist. These ratios may differ across a species range (see Fig. 12.4 and below), which the parameter *r* would not reveal clearly! *Trypoxylon palliditarse* is a type (ii) species at the core but (iv) at the edge of its range, so forming a population sink. But yet a further layer of dynamics exists. For (i), *Aphis* is a mass migrant, most *Tipula* non-migrants, but *Manduca* is an HISC species. Then, HISC leads to wide juvenile distribution and risk spreading (den Boer, 1998) in hawk moths, but to high parental care and central-place foraging in aculeate Hymenoptera. The 'themes' may not be so limited!

Traditional dynamics being time-dependent, populations and factors affecting them are estimated or modelled through several sequential generations. But if we wish to compare the results of dynamics of different species, their time-independent outcome, essentially their LHS as in point 3, is revealing as above. This is embodied in the cyclic budget (Section **11.4.3**). A habitat budget assumes immigration to be trivial numerically although it may not be so genetically (Gavrilets *et al*., 2000). But it *is* always zero for the global budget it was designed for (Freeman, 1976). Indeed, a global population is one receiving no immigrants, even though other ostensibly conspecific populations exist elsewhere. But we will see below that small behavioural differences can result in great changes in local and global dynamics. Examining the empirical examples in Sections **12.3.4.4(g)** and **12.3.4.4(h)**, recall from above that insect species show much variation in the pattern of births and deaths in relation to the distribution of resources and the ease with which they are found. Similarly, the population dynamics of rodents, by comparison a small but well-studied group, also show complexity (Turchin, 2003).

Natural selection proceeds against unrelenting and unreactive physical forces, (Nicholson's non-reactive factors). But against biotic factors, evolution and dynamics often involve a continuing arms race (Section **8.2.2.1**). Aggressors improve their efficiency and victims their counter measures, rarely to any real advance (Fisher, 1930; Price, 1972). Two related cases spring to mind: (i) araneid spiders evolved complex aerial webs thus trapping flying insects more effectively (Vollrath and Selden, 2007); and (ii) the development of scales on lepidopteran wings permitted evolution of detailed cryptic and mimetic patterns deceiving avian predators (Section **10.2.3.5**), but also gave them a better chance of escape from spider's webs (Wootton, 1992).

Ecologically and taxonomically *related species, not unrelated ones*, may have very different patterns of global dynamics. Thus, the sphecid wasps *Trypoxylon palliditarse* in Trinidad and *Sceliphron assimile* in Jamaica have similar spider-hunting but different nesting behaviours (Sections **11.4.3** and **12.3.4.4(h)**) that affect density and distribution: (i) *Trypoxylon* makes double-walled cells, trapping intruding *Melittobia*, the main parasitoid, in the internal space, *Sceliphron* does not; (ii) *Trypoxylon* prepupae place sand grains in the matrix of their cocoons, making them impenetrable, *Sceliphron* does not, although females often plaster the outside of the cells with extra material, as in *Eumenes arbustorun* (Fabre, 1919); and (iii) *Sceliphron*, ostensibly a more efficient migrant, emigrates when conditions become too wet, *Trypoxylon* forms sink populations. Hence *Trypoxylon*, while not avoiding wet areas, develops high density where the environment is drier and favourable, unrestrained by the attack of what otherwise would be its principal enemy. In the rainy Northern Range and Central Forest both its AF and survival are much reduced. *Trypoxylon* has peripheral sink populations, *Sceliphron* does not, having its highest mortality in dense populations (Freeman, 1977), *Trypoxylon* in sparse ones (Freeman, 1981a). *Zeta abdominale* in Jamaica also nests on rock walls in gullies if they become dry (Freeman and Taffe, 1974) and has a landscape pattern of dynamics like that of *S. assimile*. These are fundamental variations. A few behavioural differences have far-reaching population outcomes (Lima, 1998). Gross (1993) reviews several other cases of such differences between related species that affect susceptibility to parasitism. One presumes that the varying abilities of several *Melanoplus* spp. to resist attack by *Blaesoxipha* (Section **10.2.3.9**) will have basic effects on their dynamics.

The landscape dynamics of gypsy and lackey moths (Sections **5.2.1.4(e)**, **5.2.1.4(f)** and **12.3.3.1**), which are in related families, are quite different. This is due to the great disparity in female flight capability. Similarly, the dynamics of two abundant, widely distributed *Pieris* butterflies (*P. brassicae* and *P. rapae*), which are oligophagous, itinerant species ranging through the landscape (Baker, 1978), must be quite different from the rare and localized *P. virginiensis* (Cappuccino and Kareiva, 1985) and the wood white *Lepidea sinapis*. The former confines itself to localized patches of the food plant *Dentaria diphylla*. The difference in flight behaviour may be due to variation at the *pgi* locus, as in *Colias* (Section **10.2.4.1**), another pierid butterfly.

Similarly, the great disparity in the landscape densities and distributions of sub-generically related *Tipula* s.s. (Section **11.2.3**) suggests different dynamics. In *Acutipula*, both *T. maxima* and *T. fulvipennis* have semi-aquatic larvae that desiccate at similar rates. But the latter's adults are better, wide-ranging fliers, desiccate at less than half *T. maxima*'s rate, and find isolated wet patches in woods. These never contain *T. maxima* (Freeman, 1967b, 1968). Brown (1984) reasons that common species in the landscape use less specialized ecological resources, while those species whose needs are met at few points will have low landscape density. But at Matley *T. fulvipennis* is simply a better searcher, found in all five habitats (see Section **12.3.3.2**) while *T.maxima* is confined to one. Even within a species, some strains of a parasitoid may or may not provide biocontrol, often because of different searching power: their dynamics differ. So the expectation that phylogenetically similar species should have similar dynamics is naïve. In an applied perspective we recall (Section **12.3.4.4(h)**) that when a crop is grown more extensively its pests reach greater densities, as with *Meligethes* beetles and *Dasineura* midges. When volunteer patches of crops start to appear all over the landscape, there are more resource patches for searchers, rather as in the *T. fulvipennis* case.

Southwood's (1977) paper brings together *r* and *K* selection, the landscape distribution of resources and diverse dynamic mechanisms, an amalgam of evolution, pattern and process. But was anything significant omitted? His model is not global, it relates to habitats, adjacent habitats and their populations, while birth and death rates are obscured in the parameter *r*, the mean intrinsic rate of increase. In a global model, one must describe how these rates, estimated separately (Section **12.3.1**), are distributed from the centre to the edge of distribution and show that *r*-species are likely to have greater losses during redistribution than are *K*-species. These have quite different patterns in the above wasps. For *Sceliphron*, the AF is similar at the population centre and edge. But the edge is occupied only in the dry season, reproduction intermittent and fecundity sustained over a period is low, while juvenile mortality only ~20%. Centrally, breeding is continuous and such mortality can be >60%. *Trypoxylon's* dynamics are classically Thompsonian, high AF and low mortality in the centre and vice versa at the population edge. Seasonal changes in rainfall probably affect the density of suitable breeding sites, as in *Asphondylia* (Section **12.3.4.4(g)**) and many mosquitoes.

The balance between the major dynamical components: fecundity, juvenile mortality, sex ratio and redistributional losses are embodied in the logarithmic cyclic budget. When these are adequate in space and time (Freeman and Mulder, 2019) they quantify the specific dynamics of a focal species. Their basic tenet is that over time there is balance in that births equal deaths. If they do not the species becomes extinct and disappears from our investigative view. So it might appear that a cyclic budget provides an adequate description of an insect's LHS. All the major components are estimated. But there are some omissions: (i) being time independent the budget cannot include the time to first reproduction that Cole (1954) showed to be a critical parameter in population increase; and (ii) an individual's size, which correlates with such time and varies by a factor of >1 million in insects (Hamilton, 1995), is not taken into account.

12.5 Population Dynamics and Integrated Pest Management

Finally, we consider the relevance of population dynamics, both mathematical and empirical, to IPM. I agree with Berryman (1991b) who argues that it provides the proper basis for pest control. IPM is '… essentially applied ecology' (Waldbauer and Friedman, 1991). But there are two schools of thought (Walter, 2003): (i) the empirical school, which is sceptical that mathematical models have much practical use; and (ii) the theoretical school, who regard them as the proper underpinning in applying biocontrol. So we consider here classical biological control, augmentation of native natural enemies and conservation biological control under the IPM umbrella. At the start of the next chapter we review four ecological topics, and further integrate ecology with agriculture in its broadest sense throughout that chapter.

13 Applied Ecology and Methods of Control

13.1 The General Ecology of Pest Insects

> But one thing is certain. If man does not manage his biology it will manage him.
>
> Thomas Park, 1962

13.1.1 General introduction

Both autecology and community ecology are essential disciplines for improving agricultural, horticultural and silvicultural production, for managing pests and conserving, or better, *improving* the rural environment. Autecology provides the structure for pest control (Berryman, 1991b, 1999). Both individuals and, to an extent, the landscape can be altered to reduce their destruction (Section **13.2.1**). As Nicholson (1933) pointed out: '… the function of economic control is not to bring under control a pest that was previously uncontrolled, but to modify the control so that the density of the pest is reduced to a point at which the economic damage caused is negligible'. But demographic approaches as in Section **11.5** have not given us the insights expected (Walter, 2003). Future development requires integration of agriculture and conservation (Macdonald and Smith, 1990). It is here that community ecology is needed. The 'environment' is not something outside agriculture (Williamson, 1992). Economics aside, only persons with a deep, practical understanding of ecology should oversee modifications to these production systems. Here, knowledge of hydrology and soil science is often necessary, but the field ecologist, like the general practitioner of medicine, must be conversant in many disciplines. Hence today, foresters, farmers and land owners should be well read in ecology. Our lands are too valuable to be left to persons who are not. Would we waive the training of physicians and pharmacists?

The physico-chemical and biotic processes that occur in natural communities continue unabated in the agro-ecosystems derived from them, but are modified in some degree by cultivation and husbandry. This prevents the seral progression that would otherwise occur in the biotope in question (Section **2.2.3**). Ploughing and grazing suppress the weeds that comprise the first seral phases that would lead ultimately to the climax community typical of that biome. The grasses and low-growing plants that survive become a compact sward. Adding fertilizers and other agro-chemicals is another modification. Viewed ecologically, sustainability is lost and environmental degradation has occurred if an ecosystem failed to return to its former state were agriculture terminated – the 'Grapes of Wrath' scenario (Section **13.3.2.2**). But 'stability' and 'sustainability' have several meanings (Pimm, 1984; Grimm and Wissel, 1997; Section **11.3**). In agriculture, sustainability means continuing production, preferably at increasing levels of quality and quantity. But apart from nitrogen fixation by legumes, since the organic products and their mineral contents are removed for sale, the latter must be replaced. This is quite different from what happens in natural ecosystems. In the long term, agriculture has been subject to climatic changes discussed in Section **2.2.2** and more recently by global warming, especially in the Northern Hemisphere (Cammell and Knight, 1992; Reddy and Hodges 2000; Parmesan 2006).

Agriculture is the world's major industry. It extends over ~126 million km^2 of the Earth's land area of 560 million km^2 (68 is arable, 34 million pasture and rangeland and 24 million orchard and vineyard). So modification of the original biomes is globally extensive. When it is locally intense or more frequent, as in vegetable growing, the greater the effect on the insects and other animals that lived there. By contrast, in silviculture of broad-leaved forests, in which there is no clear felling, this effect is small. But there is much degraded wasteland about, you see it particularly from a train, close

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up and personal. A recent estimate is 385–472 million ha (Leakey, 2009). Much of this, with sufficient will, could be made beautiful, recreational and/or productive, especially for biofuels, and would minimize further deforestation and complement conservation biological control (CBC) (Section **13.2.4.7**).

Traditionally, the greater the loss of plant diversity in a landscape and hence the greater the density and/or spatial extent of a given crop, the less the expected stability of the ecosystem affected. This expectation arose out of comparing ecological communities with information systems (MacArthur, 1955; Section **9.4**) and given further support from work on *Epirrita* in Fennoscandia (Haukioja, 1980). Conversely, the greater the number of potential interactions, the greater will be the expected population constancy. One aspect of instability is more pest outbreaks (Elton, 1958; Southwood and Way, 1970). Thus, in forest *Pristiphora* (Section **5.2.1.3(e)**) some tree species reduce the ability of two tachinid parasitoids to find their host (Monteith, 1960). So one expects that monocultures need the most care. Arthropod populations in a variety of orchards and fields have greater annual variation than those of natural habitats (Woolhouse and Harmsen, 1987). And from Lawton's (1983) work on plant architecture, crops of more complex plants, like apples and olives, should harbour more species with less fluctuation of their populations than those of more simple plants such as cereals.

Some of these expectations, but not Lawton's, have been questioned (May, 1973; van Emden and Williams, 1974; Pimm and Lawton, 1977; Price *et al*., 1980). Models indicate that food web stability should *decrease* at a critical point as the number of links increases, especially if they are strong. Such links may well be inversely related to the *total number of interactions* (Margalef, 1968). Cornell and Hawkins (1995), in an extensive survey, found little difference in patterns of juvenile mortality in insect species in natural and cultivated areas. But the *natural species* sampled in their study were largely those with dense populations and hence more comparable to those of pests (Section **9.4**). May's analysis also suggests that if species are organized into 'blocks' instability is less likely. But modern cultivars, often having greater biomass and reduced defences, may allow denser populations of insects than those on better defended wild plants, another bottom-up effect.

In animal husbandry, the greater the biomass density of livestock, the greater the risks of direct attack from insects (and the diseases they transmit), infectious diseases and environmental degradation. Ants aside, high stocking levels of sheep reduce the soil fauna (Hutchinson and King, 1980). But pests are often denser under such conditions (Brown and Gange, 1990), and biting flies tend to concentrate there. Then, livestock may 'amplify' human pathogens (Section **7.3.2.4(f)**). So the type of agriculture practised impacts the agrarian population. Labour-intensive systems in the tropics involve a high proportion of the population, as they did formerly in temperate regions, resulting in dense settlements. People become more vulnerable to insect attack just as dense populations of livestock do. Dense urban populations, especially those in satellite shanty towns, suffer the same effect. While city centres are hostile to insects (Taylor *et al*., 1978a; Rubio *et al*., 2013), the suburbs are less inimical (McKinney, 2008). Highly mechanized agriculture results in low-density agrarian populations and a healthy human environment, at least from the medical standpoint.

To an extent, we hold the ecosystem in trust. We must learn to navigate in the best way possible, for production, conservation and aesthetic value. But we are only partly in control, especially when severe weather intervenes. We can steer the ship but cannot control the seas. Our emphasis may need to be shifted from what we *wish* to achieve to what ecological systems will *permit* us to achieve (Walter, 2003). In relation to aesthetics, it is not necessarily true that unmodified environments are the most pleasing. Intelligently modified environments promote conservation as well as production. Recall the beauty of many country estates and floristically rich grazed down land. In some areas, cultivating the rich valleys and leaving hillsides under woodland enhances soil fertility and is scenically beautiful. But ignorance and avarice are too often in action.

Transport of plants, plant products and livestock for processing or to the market is a further consideration. Plants transport native and exotic insects and pathogens with them and those in new areas may be vulnerable to pests and diseases not found in their place of origin. Quarantine methods are but a partial barrier as they are <100% efficient (Aluja and Mangan, 2008). A friend who manages importation of agricultural machinery told me he once found an entire nest of live bees in a crate of combine harvester parts! And many pests are highly migratory. Long-distance movements of locusts and diamond-back moths can rarely be contained, while thrips frequently sneak a ride in packaging. Nor in many countries is legislation aiming to protect native biota in place (Strong and Pemberton, 2000).

We saw in the species-abundance distribution (SAD) that while few insect species are numerous (see Fig. 9.4), serious pests belong here by definition, giving some support to the bottom-up concept of insect population control (Section **10.1**). But pest insects are often rare outside a crop, and/or become pests only when a new crop is introduced, as in Colorado beetles on potatoes, *Colias* butterflies on lucerne (Stern *et al.*, 1959), and rape blossom beetles (Section **6.2.1.2(a)**). Crops are a huge resource base. Even so, many pests in agriculture and forestry are not numerous all the time, showing that other forces are at work. Parthenogenesis is frequent in agricultural pests, which may relate to the more stable crop environment (Hoffmann *et al.*, 2008), and their high rate of increase means they can reach damaging levels quickly. Some insects, such as *Plutella xylostella*, *Nilaparvata lugens* and the tortricid complex on apples, became pests only because of insecticidal misuse (Stern *et al.*, 1959; Heinrichs and Mochida, 1984; Walter, 2003). But minor pests generally outnumber major ones (van Emden and Service, 2004; Section **9.4**). They exist in the crop or elsewhere in low numbers, or at least at levels where they cause minor economic damage, that is, they are below the *economic injury level* (EIL). Some cause little loss, others attack infrequently. But outbreaking species such as locusts (Section **5.2.1.1**) and some forest moths (Section **5.2.1.4(c)** to **5.2.1.4(g)**) have drawn much attention here, making forecasting essential. Outbreaks of insect vectors such as anopheline mosquitoes and simuliid flies, and in train the diseases they transmit, are also usually sporadic.

Insect populations vary in the basic dimensions of time and space, as in Andrewartha and Birch's plot of Australian locust numbers (Section **12.4**; Fig. 11.7), or in the theoretical distribution diagram (Fig. 12.4). Apart from killing pest insects directly, denying them resources in either dimension is fundamental. Our knowledge of pest dynamics is uneven. In forests, orchards and field crops the dynamics of herbivorous insects are well investigated (Cornell and Hawkins, 1995). But in the medical and veterinary spheres these processes have by comparison been little studied. Regrettably, our knowledge of the natural dynamics of insectan predators and parasitoids is fragmentary (Hassell, 1969; Danks, 1971b; Freeman, 1973a, 1977, 1981a; Freeman and Ittyeipe, 1993; Sisojevic, 1975; Luff, 1982; den Boer, 1998), although this would provide a more informed basis for applying biological control. While diverse practical means exist of modifying pests' biotic environment, with the exception of irrigation, mulching and drainage, little can be done to alter their gross physical environment.

Explanations of what determines the levels of pest numbers will be biased by one's view of the theories of population. Even given adequate empirical data, theory guides perception (Carr, 1987; Margolis, 1993). But a simple approach is to regard climatic favourability at a given place as the ultimate factor setting the mean level about which insect populations vary (Section **12.3.4.4**), the 'harsh and kind' environments of Andrewartha and Birch. Nicholson's explanation is rather different, centring on various forms of competition (Section **11.2.2.2**). Weather patterns, his legislative factors, alter but do not regulate numbers. On the other hand, enemies (Berryman, 1999) often drive numerical fluctuations of pests in a 'top-down' manner. Nicholson regards this as their competition for victims, as shown by the practical experiments of successful, classical biocontrol (Section **13.2.4.6**). But as Milne points out (Section **11.2.2.4**), harsh or catastrophic weather may cause major mortality at any time, as with rainstorms on Colorado beetles and aphids. Where resources, especially quality food, are abundant, a period of favourable weather allows rapid population increase, especially in *r*-species with short life cycles and high fecundity. Enemies often fail to restrain them (Southwood and Comins, 1976). Mosquitoes and aphids are prime examples. Milne's theory gives a simple way of looking at a pest population in a given habitat, such as a field crop. But on the wider scale of the metapopulation that crops often form, it is inadequate since migration, which in many species is highly significant (below), is not considered.

As we have seen, while some pests are localized and have poor redistributive powers (carrot root flies [Section **3.2.2.1(i)**], Colorado beetles [Section **5.2.1.2(c)**] and gypsy moths [Section **5.2.1.4(f)**]), whereas others (locusts [Section **5.2.1.1**], diamond-back moths [Section **5.2.1.4(a)**], many aphids [Section **5.3.1.2(h)**] and *Manduca* hawk moths

[Section **5.2.1.4** (**i**)]) are highly mobile. Although Southwood/Comins' synoptic model (Section **11.2.2.5**) was welcome in including selective modes, classical *r*- and *K*-selection does not entirely distinguish these groups (Greenslade, 1983; den Boer and Reddingius, 1996; Sections **10.2.4.1** and **12.3.4.4**(**c**)). Even so, natural control must be very different in these selective modes and needs a different approach when devising economic control, especially by biological methods (Section **11.2.3**). Spatially extensive data are required (Thompson and Parker, 1928a; Brewer and Gaston, 2003).

Since physico-chemical and biotic aspects of environment may be inimical to pests, these are the major factors we can modify or supplement to combat them, although many interactions exist (Sections **10.1** and **12.3.4.4**). For physical methods, temperature can be controlled only in greenhouses and silos (below) or by choosing aspect. So the main methods of use are hydrological and mechanical. Flooding kills pests in the soil. Irrigation may reduce the reproductive success (RS) of field pests, as in diamond-back moths (Tabashnik and Mau, 1986), and/or mitigate the effect of their herbivory. For some crops, especially tropical ones such as rice, bananas and sugar cane, it increases production, but may enhance populations of aquatic Diptera, especially mosquitoes, that vector disease (Pennisi, 2001; van Emden and Service, 2004; Section **7.3.2.4**(**c**)). Water resources must be modified to combat them. Mechanical methods include traditional tillage, which causes direct destruction, desiccation and limits pest movement. It often exposes pests in the soil to avian predation, an interaction with a biotic factor. Some crop varieties have greater physical protection in surface toughness and siliceous inclusions (Section **2.4.2**), but these and their many chemical defences are often less in high-yielding cultivars. Finally, the application of organic poisons, even those such as pyrethrum and microbial toxins from biological sources, fall under this broad physico-chemical heading. Physical factors may also be used to influence biotic ones (below).

For biotic methods, the top-down/bottom-up debate is a recent aspect of insect population control. Is destruction by enemies or by shortage of quality food (Sections **10.2.2.5** and **12.3.4.4**) of greater importance? While lower quality food reduces AF and survival of insectan herbivores in the wild (White, 1976, 1993; Awmack and Leather, 2002), it is to an extent debarred as a viable control strategy in food crops in which quality in quantity is the prime aim. Indeed, high-yielding cultivars of rice usually lose a greater percentage of grain to pests than do traditional varieties (Thacker, 2002; Section **13.3.2.2**). While maize cultivars resistant to boring larvae (Section **4.4.3**) need not have poor cobs, they cannot be grown everywhere. In many crops, the development of bottom-up effects in resistant varieties is also constrained by appearance and palatability. So we often rely on top-down systems of biocontrol or other biotic methods, such as trap cropping (Hokkanen, 1991). However, if food is nutritious and plentiful, the pest's enemies, like the pests themselves, may thrive and assist control.

Top-down methods famously include biological control, not only the classical use of exotic enemies, but also modifications of the crop and its environment to enhance the effects of indigenous enemies. The latter method is the most eco-friendly of all. Using other living biological agents, like fungal and bacterial pathogens, is a further example. Our control of temperature and humidity in enclosed spaces such as glasshouses and grain silos not only influences the crop directly, it also allows us to manage the way in which pests interact with their enemies. In the former case, while conditions for rapid plant growth must be maintained, they may be adjusted to deter a pest but favour its enemies, as in the famous and continuing case of *Trialeurodes* by the parasitic wasp *Encarsia* (Section **11.2.1**). Control of the gases in grain stores, largely by increasing CO_2 levels, comes in this category. Interestingly, Iron Age Britons often stored their grain in covered pits where the depletion of oxygen and production of CO_2 by respiration must have deterred potential pests. Also, appropriate atmospheric modifications can be made in glasshouses when workers are absent. For grain, however, blowing warm air through it on sunny days, so drying it to meet moisture standards and deter pests, is often used.

A central problem for pest control is individual variability (Łomniki, 1988); in den Boer's terms pests spread risk (Section **9.7**). For example, in the economic control of codling moths (Section **6.3.1.1**(**g**)) some larvae may already be protected inside young apples when an insecticide to kill eggs and young larvae is applied, and some late females have yet to oviposit. Strangely, in northern New Zealand, there are several, well-synchronized generations of this moth (van Emden, personal communication). In Europe at least, its pupation sites are extremely various. Variation, as Darwin and Wallace saw, and Fisher developed, provides the raw material of evolution (Sections **9.1** and **9.6**). So *any control measures* we undertake face individual variability and will have evolutionary outcomes unless the pest is entirely eliminated (Gould, 1991). That has seldom been done, counter examples being screw worms from the USA and North Africa (Section **7.4.1.2(d)**), melon flies from the south-western islands of Japan (Section **6.3.1.1(o)**) and *Anopheles gambiae* from Brazil (Section **7.3.2.4(d)**). All have required huge expenditures.

Predictability is a further point (Section **10.2.2.2**). While predictable factors occur in ecology, often driven by solar regularity, they are not always linked to pest outbreaks, which for practical purposes need to be foreseen. Then, if control measures are required, they can be planned in advance, so avoiding insurance spraying. Forecasting methods include using day degrees (D°) (Section **10.2.2.2**), monitoring winter temperature, and scouting, trapping and knowledge of vulnerable periods in the pest's life cycle. Thus, mean February temperature is a good predictor of *Myzus persicae* numbers in late spring (Leather *et al.*, 1993), and damage from leather-jackets (Section **3.2.1.2(f)**) in May is likely if adults were numerous during a previous wet, mild autumn.

We examine below some general ecological and other principles of pest control and revisit a few specific examples covered in greater detail in Chapters 3 to 7. Because of increasing public interest in the environment we now appreciate that farms are not just places for growing crops and livestock to maximize production and profit, but an inclusive part of our ecosystem, albeit privately owned, but probably for the best. Optimizing the needs of economics, with its pernicious tenet of ever expanding profit, and the imperatives of social well-being, aesthetics and ecosystem sustainability, will not be a simple task. Pearce *et al.* (2007), however, see economics as part of the solution to conservation in that conserved areas may be used to generate wealth in various ways. But an informed input from the consumer, the baseline of democratic society, is essential.

13.1.2 Four ecological topics relating directly to pest control

Before considering the direct application of ecology to control pests, there are four general areas to examine.

13.1.2.1 Population structure: Univoltinism, multivoltinism and risk spreading

In the tropics most insects are multivoltine and many breed all year round, when hygrothermal conditions allow. But from desert areas to Mediterranean and temperate zones the proportion of multivoltine (q.v.) species decreases and, of course, those showing univoltinism increases. Many multivoltine species from warm-temperate regions are univoltine in mid-temperate ones, while univoltine species in these zones often take two or more years to develop as they approach the Polar Circle. There are almost no insects that breed in winter, because temperatures are near zero or sub-zero. While some larvae living in the soil may develop slowly, reproduction itself is exceptional (winter moths, see Section **5.2.1.4(g)**, some trichocerid flies).

Obviously, multivoltine pests tend to have short life cycles and so have the potential for a rapid build-up of numbers, generally making it difficult to restrain them. Of all orders, Diptera usually have rapid development (Section **10.2.2.2**). Tropical mosquitoes are a prime example: *Aedes aegypti* may develop from diapausing egg to adult in ~1 week. Even in temperate regions sheep strike flies, *Lucilia* spp., develop quickly. A dead lamb carelessly discarded in spring and found by a few females provides food sufficient to produce many thousand adults within a few weeks. Other calyptrate Diptera such as stable flies and house flies, some sawflies and Colorado beetles are further examples of temperate pests whose populations may breed rapidly.

Another effect associated with multivoltinism has important consequences for risk spreading in the pest and hence for its economic control. Because not all individuals start to reproduce at the same time and because individual rates of development vary, within only two or three generations all stages of a pest may be present together. Rapidly developing lines will be represented by young adults, slowly developing ones by juveniles and perhaps by old adults of the previous generation. Hence, a given mortality factor or control strategy aimed at a vulnerable stage will not affect all individuals. They have spread risk in time (Section **9.7**).

In most Endopterygota, unlike many Exopterygota, spreading risk in time leads to spreading risk in space. Using the example of *Lucilia* again, the adults will be searching for mates or on their several different food sources and oviposition sites, the eggs and larvae will be on several carcasses while the pupae will be in the soil at some distance from their former food. A similar scenario is seen in hawk moths, except that the progeny of a single female will be even more scattered. Hence in such examples, not all individuals will be vulnerable to a single mortality factor or control strategy, simply because they are in different places.

Conversely, there are vulnerable stages, those weakest links, where control can be applied. For example, in chemical control of many stem and fruit pests (Sections **4.1** and **6.3.1.1**), the weakest links are the periods of oviposition, when eggs are being placed externally and when young larvae are boring into the plant, as in *Ostrinia* (Section **4.4.1.1(d)**). We consider below some specific examples of how the presence or absence of temporal and spatial risk-spreading affect economic control measures. For herbivores, note that the plants themselves may spread risk, as well as their pests. First, some examples of low risk spreading.

In south-east England, *Apion dichroum* (Section **6.2.1.2(a)**) is univoltine. At some time in May according to season, the weakest link in their life cycle occurs, as nearly all individuals are post-migratory, flightless adults in the clover fields, the females preparing to oviposit in the newly opened flowers. A single spraying with a short-term insecticide at this time may give satisfactory control for the year (Freeman and Wimble, 1970). No later immigration can occur. The weevils cannot spread risk in time as they use a large, specific, ephemeral and annual reproductive resource. Even so, small marginal population units still occur in isolated patches of wild clover, so that there is some spatial risk spreading. This pest cannot be eliminated entirely.

Similarly, warble flies in winter occur as third larval instars under the hide of cattle, a very localized food resource and one very accessible for control. If they are all killed at this time the pest would be eliminated. Years ago this was done by a co-ordinated effort on Cyprus, when the farmers there simply squeezed them out, and the fly went extinct (Section **7.4.1.1(c)**). Indeed, warble flies are now extinct in many European countries. Colorado beetles are unusual endopterygote pests, since all the stages are found together feeding on the food plant or as eggs and pupae attached thereto: there is little spatial risk spreading. And they all overwinter as adults in the soil. With its high visibility and the presence together of all stages one would think that the species would be vulnerable to insecticides. Trouble is, they have become highly resistant to most of them.

In many Diptera Nematocera (*Tipula*, gall midges, biting midges, mosquitoes), the adults are short-lived and hence at any instant their great majority is juvenile. Looking at the important case of tropical culicid vectors, adult females may have death rates of the order of 0.20/day or higher (Sheppard *et al*., 1969; Mogi, 1984; Chmielewski *et al*., 2010), although in the notorious *Anopheles gambiae* this rate is lower. At the above rate, a cohort of 100 emerging on day 1, will number 80, 64, 51, 41, and 33 over the next 5 days and reduce to ~20 in a week. So the longer the pathogen takes to develop in the vector, the lower its chances of transmission to a new host. Meanwhile, if 100 new adults emerged each day there would be a considerable dilution of older by younger adults. While fogging to kill adults is essential (Section **13.4.1**) it has little short-term effect on population size. Fogging every day curtails oviposition if the population is not vagrant, but a better overall strategy is to deny oviposition sites. With *Aedes aegypti*, which often breeds in discarded domestic receptacles, this means organizing a comprehensive social programme of cleaning up waste cans, bottles, tyres and other containers (see Fig. 7.9; Section **7.3.2.4(f)**). But it is difficult to induce people to practise such simple control measures, many simply refuse to believe that aquatic mosquito larvae have anything to do with aerial mosquitoes.

Mosquitoes and sand flies are nuisance biters at tropical beach resorts. Tourism to such venues is a highly competitive. Fogging in the evening would inconvenience tourists at dinner time, one might eliminate the tourist more easily than the mosquito. After all, if you live in Toronto it is just as easy to fly to Barbados as it is to Cayman. Besides, fogging, for the above reasons, has little effect on the extant adult population unless done daily. Destroying breeding sites, so reducing carrying capacity (Section **12.2.3.3**), is a far better strategy,

13.1.2.2 Reservoir populations, redistribution and their effects on control methods

An extension of the idea of spatial risk spreading in a pest is where some parts of its fragmented population exist in places outside the farmer's control. So the pest may migrate onto the crop from wild food plants or volunteer crop plants. Of course, pests on a crop are not always controlled, but there is some prospect of reducing their numbers to an acceptable level, whereas excepting invasive methods of biocontrol, those in a reservoir population are generally outside economic control. Similarly, in animal husbandry, flies causing myiasis (Section **7.1.1.3**), for example, occur on wild mammals and even on domestic waste food. In medical situations there are zoonoses (Section **7.2.2.2**(**b**)), which are comparable to reservoir populations in agriculture.

The agricultural importance of reservoir populations, especially polyphagous ones, depends on several factors that operate complexly. First, we must determine if our pest is truly polyphagous, not a group of cryptic species (Section **1.3.4**). Second, truly polyphagous pests, like many wireworms and cutworms, have a wider, more fragmented distribution outside a given crop than do specialized pests, such as Colorado beetles, since they feed on a greater variety of plants. They form a *metapopulation with a diverse resource base* (Sections **9.5** and **12.3**). So when a crop vulnerable to a polyphagous pest is planted in a given locality, it is probable this pest has a reservoir population nearby. This may allow a build-up of its numbers early in the year, before the crop is available, so if possible control should be applied at a landscape level. But such a pest may migrate from great distances. Thus, in Australia, *Heliothis punctigera* (Section **6.2.1.2**(**d**)) flies hundreds of kilometres from arid, central areas, where it feeds on wild plants, to the fertile crop-growing areas of the east coast (Walter, 2003). Such pests may well have low resistance to insecticides, however, since they are never exposed to them and so be killed by low doses. Third, crops such as wheat and cotton that cover extensive areas are more likely to be found by migrants than intensive horticultural ones, just because they are bigger targets. Finally, the ability of a pest population to search and find a new food source (the crop) depends on the searching ability of each individual (its individual searching capacity – ISC) multiplied by the number searching. Localization of search is also a factor. Here we are usually concerned with adults seeking reproductive resources. Thus, a Colorado beetle has lower ISC than a hawk moth like *Manduca*. But many important crop pests such as aphids and fruit flies, while having a low ISC, occur in vast numbers. They are *mass migrants* moving prodigious distances high in the air while suffering great mortality (Section **10.2.4.5**). If they hit a cold front, or at the end of the day when thermals cease, they fall from the sky like snowflakes.

On the other hand, many small pest insects have absolutely poor dispersive power. They fly slowly for short distances and remain near the ground (Section **12.3.4.4**(**c**)). Carrot root flies and clover seed weevils are examples. These weevils generally travel only 200–300 m from the clover fields to the overwintering habitat (Freeman, 1965). Carrot root flies fly short distances (Jones and Jones, 1984) from vegetation to the adjacent crop. While their larvae can feed on wild Umbelliferae (Fig. 13.1), control in a given year is likely to have a measurable effect in suppressing numbers in a subsequent year. The few flies that arrive result only from adjacent farms and reservoir plants that managed to survive from the previous year. But such localized populations may develop local resistance to insecticides as Colorado beetles have done famously.

Different resource-seeking activities lead to different types of egg distribution (Section **10.2.4.7**) and in turn to that of a subsequent juvenile stage, the latter finally relating to the duration and distribution of resources (Section **12.2**). They can be classified as follows:

1. Reproduction on the natal food patch, all the eggs of a given female being laid in one place (winter and gypsy moths).
2. Oviposition in the natal patch followed by dispersal of a now lighter female, who may survive to deposit eggs elsewhere (*Tipula paludosa*, *Choristoneura fumiferanae*).

Fig. 13.1. The wild carrot, *Daucus carota* (Umbelliferae). Further plants in the background provide more reservoir patches for carrot root flies.

3. A single long flight prior to reproduction, then resource location within a patch and no further movement from it. Here the patch may be large enough for the needs of one or several females, who may then lose the power of flight. All the progeny of a single female are deposited in one place, although not often in one batch (clover seed weevils, several aphids, Heteroptera such as *Nezara*).
4. Pre-reproductive flight followed by finding several resource patches: eggs are deposited in variably sized batches in different places far apart (*Manduca*, *Anastrepha*, *Calliphora* and *Lucilia* spp. see Section **12 3.4.4(c)**).

So, polyphagy coupled with pest mobility has basic outcomes for economic control. Similarly, refuges can be used to manage crop pests. Alstad and Andow (1995) consider this matter in a model, using a maize/*Ostrinia* system (Section **4.4.3(b)**). They conclude that a patchwork of transgenic and susceptible fields (refuges) slows the development of resistance and saves money (see also Gassmann *et al.*, 2009). Gould (1998) concurs, when *Bt* cultivars are used widely, as in cotton, it is understood that such a mosaic disrupts the evolution of *Bt* resistant strains.

13.1.2.3 Commonness, rarity and pest status

We noted (Section **9.4**) that while most insect species are rare, pest insects are common by definition: they form dense populations. They are either a constant nuisance like wireworms (Section **3.2.1.2(a)**), 'outbreaking species' causing only periodic damage (Hunter, 1991), or somewhere in between. Simply because there are great numbers of insect species (a few million), the total number of pest insects is appreciable (a few thousand). But insects are unusually pests. Some questions thus arise: (i) Why are many pest species dense on crops, but sparse in natural environments (van Emden, personal communication)? Thus their comparative dynamics are of special interest. (ii) Why is it that some families, like pierid butterflies, have a conspicuously high proportion of common species? (iii) What is the status and occurrence of outbreaking species? (Hunter *et al.*, 1991; Myers, 1998). (iv) Are there genetic reasons for commonness and rarity and hence pest status, since closely related species often differ markedly, as in the *Tipula paludosa* group in the UK (Sections **12.3.4.3(e)** and **13.2.2**)? Apart from (iii), we have satisfactory answers to none of these questions.

Several authors have considered outbreaking pests. Of course, the size of these populations depends upon the extent of the outbreak area: is it an extensive part of a biome or more restricted (Section **12.2.1**)? In fact, truly massive outbreaks occur in only two situations and three groups: (i) Locusts (Rainey, 1951; White, 1976; Cheke and Holt, 1993; Lecoq, 1995; Showler, 1995; Ceccato *et al.*, 2007) and armyworms (Betts, 1976; Odiyo, 1979; Rose *et al.*, 1985), both groups being associated with sub-tropical grasslands; and (ii) Moths in mainly temperate forests (Wallner, 1987; Hunter, 1991; Berryman, 1996; Myers, 1998; Bjornstad *et al.*, 2002; Nealis and Regniere, 2004). Billions of migrants build up over a few years in extensive source areas. Massive movements of *Heliothis* spp. (Section **6.2.1.2(h)**) must also be mentioned. These moths, like locusts, outbreak in arid regions after sporadic rain and emigrate in response to crowding and drought. Comparably, where huge areas of a crop are grown, a few specific pests become numerous and troublesome. They include *Diabrotica* beetles and *Ostrinia nubilalis* on North American maize, *Meligethes aeneus* on European oilseed rape and *Nilaparvata lugens* on South-East Asian rice. Large-scale migration is key here (Drake and Gatehouse, 1995). Locally ruinous, although rather smaller, infestations occur when small migrating species, such as aphids, diamondback moths and acalypterate cereal flies encounter cold fronts and fall from the sky (Section **13.1.2.2**).

The above cases involve extensive grasslands, grain crops and forests. Recall that plants ancestral to our vegetables occur sporadically in the wild. Those in the Cucurbitaceae, Cruciferae, Solanaceae and Papillionaceae (Section **2.1**) rarely comprise extensive areas. They are opportunistic vagrants in space and time, form part of a temporary sere, or occur on disturbed soils (Price *et al.*, 1980). The insects that fed on them originally needed good searching capacity. So we expect that when such crops are grown extensively they may be attacked severely as they form large targets for such species. This applies whether the pest's strategy is *en masse* searching, as in *Plutella*, or requires high ISC (Section **10.2.4.1**) as in *Manduca*. Extensive damage may ensue if controls are not deployed rapidly. Then, unlike oaks and conifers, tropical trees are typically isolated (Janzen, 1970, 1981), so if they are grown in extensive plantations, as teak often is, damage is to be expected.

The dynamics of rare species are poorly researched (Eickwort, 1977; Jayasingh and Freeman, 1980;

Price, P.W., 1997). While they are not pests, if we knew more of their dynamics it might well, by comparison, throw those of abundant pests into clearer focus. In Jamaica, the rare *Monobia mochii* has a lower AF and more restricted distribution than related wasps that are common (Ittyeipe and Taffe, 1982). Similarly, the swallowtail *Papilio homerus* is found in only two small areas of wet forest, its food plants being two species of the tree *Hernandia* (Garraway *et al*., 2008). But there is higher juvenile mortality in disturbed rather than in virgin forest. In the UK, several butterflies on the northern edge of their range have localized habitats too, for example *Papilio machaon* (Dempster *et al*., 1976), the Lulworth skipper (Thomas, 1983) and the large blue (Thomas *et al*., 1998). But there are many species that are uncommon *and* widespread, for example the mosquitoes, *Aedes dorsalis*, *Culex molestus* and *Theobaldia subochrea* in England (Coe *et al*., 1950).

13.1.2.4 Climatic change and the status of pests

The physical drivers of climate (Section **2.2.2.1**) have effects on many time scales. Although climate would be in constant change in the absence of a burgeoning human population, our activities in agriculture, industry and transport have had additional effects. Agriculture reduces forest and so CO_2 absorption, while industry and transport emit various nasty gases and much CO_2. There are spray drifts and chemical run-offs from agriculture and polluted waters from towns and industry. Forests have been greatly reduced over several millennia (Diamond, 1999; Pearce *et al*., 2007) and levels of CO_2 and other gases have increased since the Industrial Revolution (Crowley, 2000). Mean temperatures in many parts of the world have risen and snow cover and ice sheets have diminished, especially in the Northern Hemisphere. But have our activities had sufficient impact to materially alter the global climate or are these changes a result of drivers outside our control or influence, or both?

In temperate regions, models of progressive global warming predict less cold winters with more precipitation, slightly warmer, drier summers and hence a longer growing season (Parmesan, 2006). This sounds good both for crops and pests, although generally we hear only doom and gloom. What consternation global cooling, as in the Maunder Minimum (Section **2.2.2.1** and Fig. 2.3), would cause! In particular, during the past half-million years inter-glacials have been short and intervening glacials long (Shackleton and Opdyke, 1976, in Coope, 1979). But presently, more frequent and more intense heat waves are likely (Meehl and Tebaldi, 2004). For a focal pest, climate defines a region within which a complex of factors interact on it (Huffaker and Rabb, 1984; Gaston, 2009a and b), and we noted (Sections **10.1** and **12.3.4.4**) that biotic factors are generally driven by physical ones. So with climatic change many biotic changes are expected to ensue. Cammell and Knight (1992) classify these as having *direct* and *indirect* effects, a dichotomy Thompson (1929) pointed out long ago. But while it may get warmer at a given latitude, and in train this may affect rainfall, the sequence of photo-periodic changes is unaltered, except on the long time scale of Milankovitch cycles (Section **2.2.2.1**). Higher temperatures have two main direct effects on pests and other insects: (i) they allow a longer summer period in which more generations may be completed successfully; and (ii) less cold winters permit their increased survival. Indirect effects also occur. Then if climate gets warmer and wetter, it might well promote the spread of bacterial and fungal insect pathogens. And in temperate latitudes, increased diversity caused by new species spreading northwards would result in further interactions.

Apart from its effects as a greenhouse gas, elevating ambient temperatures, increased atmospheric CO_2 also affects plant metabolism directly. Global, gross primary production is expected to increase with this trend in both C_3 and C_4 plants (q.v.). C_4 plants, which are mainly monocots, have the ability to concentrate CO_2 in their bundle sheath cells (Caswell and Reed, 1975). Originally, they were expected not to be affected as much as C_3 plants (Wand *et al*., 1999), but some wild C_4 grasses and C_4 crops (maize, sorghum, cane) (De Souza *et al*., 2008) do show substantial growth responses. Consequently, all plants will increase biomass and in turn fix even more CO_2, tending to oppose further increase. They also use water more efficiently under such conditions. But while C_3 plants have increased photosynthesis, they have decreased foliar nitrogen, which in turn affects the growth of folivorous insects. The ~40% elevation of atmospheric CO_2 projected for the near future, an amount similar to that since the Industrial Revolution, would produce these plant responses.

13.1.3 A brief history of insect control: Arsenic to integrated pest management

Potential methods of pest control involve either modifying the pests themselves, which has become possible only recently, or altering their environment by physico-chemical or biological means. Essentially, it is applied ecology as Haeckel (Section **9.6**) defined it. Now, the damage pests cause is primarily a consequence of their appetitive movement towards their food. This is true whether pests originate, generally as migrant adults, outside the crop, livestock area or human habitation, or multiply within this finer spatial scale. Our attempts to protect crops, livestock or ourselves *ideally* depend on blocking or disrupting this movement. It is clearly an environmental method and a rationale that is critical in preventing the transmission of human diseases. But it can be used in only a few situations, as with insect repellents, pheromone techniques, screening buildings and silos and using mosquito nets; ultimately by eradicating the pest. Mating disruption, antifeedants and trap crops are a partial solution. A less-than-ideal but widely applicable method is to reduce pest populations to low levels, at which the damage they cause is of small economic consequence, or, where human diseases are concerned, is the best we can reasonably manage at present. The latter is illustrated by our changing view of controlling malaria. With the advent of DDT, global eradication was thought possible (Casida and Quistad, 1998); now we accept that minimization is as good as it gets. Even so, pests have been eradicated occasionally, for example *Anopheles gambiae* in Brazil, warble flies in most of Europe, screw worms in the USA and North Africa, and *Anthonomus grandis* in much of the US Cotton Belt. Here, individual methods, like sterile mating technique (SMT) and genetic modification (GM) may prove to be most useful.

Although in the West we usually think that the use of highly noxious inorganics in the pre-1940s was the start of pest control, some more subtle means had been developed long before in Africa, the Middle East and the Orient (Thacker, 2002). European efforts at controlling pests were defeated by the Christian belief that such attacks, like plague, were a scourge on the sinful (Section **11.1.2**), to be dealt with by prayer and sacrifice (Tuchman, 1978). Fortunately we, and particularly agro-chemical companies, no longer adhere to this view!

Many African peoples still mix grain with fine sand, thus potentially abrading insects, and store it in the roofs of their huts where fires dry it and smoke further deters pests (Abate *et al.*, 2000). Related techniques are currently being developed to employ inorganic dusts and particle films (Section **13.2.3.5(f)**). Sumerians used sulphur and Persians knew of the insecticidal properties of *Chrysanthemum cinerariifolium*, but Europeans did not learn of the latter until the 1850s, when small quantities began to be marketed. Over 3000 years ago Chinese people used toxins extracted from plants as seed dressings and burnt poisonous plants as fumigants (Walter, 2003). Much later, Europeans used nicotine preparations. Where crop production was small-scale, human labour was often sufficient to stem pest attack. When Colorado beetles spread across North America in the late 1800s (Section **5.2.1.2(c)**), Paris green (copper aceto-arsenite), originally a paint, was employed to kill them. If one reads an old textbook, one is struck by the abandon with which huge quantities of poisons containing lead, mercury and arsenic were heaped on the environment. Here is the method given by Comstock (1940, p. 857), for controlling apple maggots:

> It has been found that most of the flies can be killed before they lay their eggs by applying a spray of arsenate of lead, four pounds in one hundred gallons of water, during the first week of July. The flies lap up the drops of moisture from the fruit and foliage and are thus poisoned. The fallen apples should be collected or hogs allowed to run in the orchard.

Roast pork with apple sauce anyone?

Naturally, the toxicity to man of such inorganics was to an extent appreciated at the time and, as usual, doom and gloom forecast, but in most cases it seems not to have materialized. Their effects on the general environment, however, may have been considerable (Whorton, 1974). We cannot return to monitor this backlash, but their use probably formed a major component in the loss of environmental diversity that has occurred in Europe and North America over the twentieth century.

The insecticidal properties of DDT discovered in 1939 by Paul Muller, a Swiss chemist, was a watershed for insect pest control: we can think about 'before DDT' and 'after DDT'. For the first time a really cheap, effective, broad-spectrum insecticide, which is persistent, easy to store and almost non-toxic to us, was available. One of its early uses was to avert a typhus epidemic in war-torn Naples in 1944, Neapolitans being de-loused with DDT powder (Section **7.2.1.2**(**b**)). Continuing with Italy, its use from 1946–1950 led to a drop in annual malarial cases from 400,000 to almost zero. Its wide-scale application in both medical entomology and agriculture assured commercial success. When it replaced lead arsenate (see above), a great reduction in pesticide use ensued. From 1944 to 1951, DDT production in the USA increased tenfold, although even then Cameron (1945) had warned of its potential mammalian toxicity. While we now regard DDT with abhorrence, because it may cause us liver damage and be concentrated up the vertebrate food chain, it is important to place it in the context of what had gone before. But because DDT was so effective initially, other forms of control lapsed. Instead of developing cultural control in *conjunction* with new pesticides, traditional methods faded by default. In some cases DDT disrupted existing biological control, as with the parasitoids of *Icerya* in California (Stern *et al.*, 1959; Section **4.3.5**). The period from the late 1940s to mid-1960s has been called the *Dark Ages* of pest control (Kogan, 1998), although far-sighted men such as H.S. Smith and E.H. Strickland had warned of the dangers of total reliance on chemical control (Walter, 2003). As early as 1914, Melander noted that San Jose scale insects were becoming resistant to lime sulphur sprays (Melander, 1914; Andrewartha and Birch, 1954, pp. 701–703).

After DDT, the range of insecticides increased rapidly. By 1960 most of the major chemical groups now used had been discovered. But the resistance pests achieved to organochlorines led quickly to two results: (i) the application of greater concentrations of these insecticides: good for business, bad for environment; and (ii) the search for new insecticides to which the pests were not resistant. In fact, this situation revealed one of the strengths of capitalism, although at the time it was unfashionable to point it out. Some of the considerable profits made were ploughed back into research and development (R&D), so that second-generation insecticides were soon ready for sale. In the 1960s, an R&D establishment in Kent, embracing disciplines from mathematics to mycology, employed over a hundred workers holding PhDs.

Although new potential insecticides are still being synthesized, only about one in 20,000 of them finds a commercial niche. The cost of the entire process from discovery to marketing is presently of the order of £100 million. This cost has to be recouped by profit, meaning that only products with huge sales potential are financially viable. One hears that if an insecticide cannot be used against mosquitoes or vine and cotton pests it has doubtful commercial future. Expenditure on R&D, production and distribution has to be recouped during the patent period. Unfortunately, this prohibits the development of appropriate, small-scale insecticides and stifles small-scale entrepreneurship; it is the cost of environmental safety, although Big Business has not been exemplary in this matter. Casida and Quistad (1998) and Oerke (2006) give brief histories of the R&D of insecticides. Today it is not so much that new 'wonder' insecticides are needed, but that more effective ways of deploying the ones we have are developed, culminating in IPM (Section **13.3**) and its 'green' relative *CBC* (Section **13.2.4.7** and below).

13.2 Methods of Pest Control

13.2.1 General: The individual and the environment

As we noted briefly in Section **13.1.3** and following the deep structure of autecology, the means of pest control are either via *the individual* or via *the environment*. The former includes SMT as well as GM of the pests themselves. The usable environmental factors are broadly physico-chemical (insecticides included, but with increasing disenchantment) and biological. In IPM they are used in combination, and culminate in a general environmental plan of CBC. Apart from such extrinsic methods, genetic means of control, which may be intrinsic or extrinsic to the pest, are being researched increasingly (Burt, 2003). Genetic modifications of crop plants for resistance to pests (Gould, 1998; O'Brien and Mullins, 2009) are, of course, changes in the pest's environment. For the practicalities of control see Pedigo (1996) and Ruberson (1999).

With respect to human activity, pest insects occur in several broad categories. The basic split is between crop culture and medical/veterinary fields. It may come as a surprise to the student who has ploughed through this book, having had to wrestle with diversities such as insect taxonomy, physiology, ecology and behaviour, mathematical models and statistical analyses, with some history and a little philosophy thrown in, to learn that many workers in these applied areas do not talk to each other that much (van Emden and Service, 2004). This is very lazy and potentially time wasting. Teng (1994) complains of this failing even within the confines of rice-growing technology. Thus, workers on malaria and on Chagas' disease may use different terms for the same transmission parameters (Dye, 1992), illustrating the dangers of over-specialization. Following these authors' lead and the spirit of this book we take a holistic view.

The spatial scale of a pest problem is another consideration (Section **12.2**). For crops there are three areas: (i) field crops at two scales, agriculture and horticulture; (ii) orchards, vineyards and plantations; and (iii) forestry. In animal husbandry the spatial scale ranges from small dairy farms to free-range ranching of sheep and cattle. Finally, in medical entomology we must consider endophilic insects like lice and fleas to the broad areas occupied by tsetse, simuliid flies and the anopheline vectors of malaria. Since people, like insects, live almost everywhere we must aim at the global reduction of all medically important insects. Being on the same scale as the control of forest pests, or of the total eradication programmes for agricultural pests (boll weevils, screw worms), such an endeavour grades into the recent initiative of CBC (see above and Section **13.2.4.7**).

For different crops, different levels of insect attack can be tolerated. This level (Sections **3.1**, **3.2.2.1**(**d**) and **6.3.1.1**(**g**)) is least when the marketable product is attacked, as in the case of apples, much greater when it is not or when a gross product such as sugar is manufactured. The concept is embodied in the EIL (Section **13.1.1**). A further consideration for crops, livestock or man, is whether or not the pest is a disease vector. For livestock and people there is a threshold level of attack, or *biting rate*, below which the disease will die out (Section **13.4.1**). Control aims to reduce such pests so their action falls beneath this level. If the transmitted pathogen can be eliminated, however, as in the case of *Plasmodium* in Jamaica, the presence of the vector is of less concern. But unintentional re-introduction is always a threat, and in this island minor outbreaks are recurrent.

13.2.2 Individual methods

There are two methods of modifying individuals, who are then released to reduce the pest population or cause its extinction. The older method is SMT (Section **7.3.4.2**(**d**)), also called SIT, the sterile insect technique (Knipling, 1955). Indeed, releasing sterile insects of both sexes can be more efficient (Proverbs, 1969). Normally, the pest's population is flooded with huge numbers of the pest irradiated in a factory. Apart from their sterility they are, hopefully, vigorous regarding mate finding and mating. A newer method, rather than irradiate them, is to employ lethal genetic systems to sterilize females (Thomas *et al*., 2000). In all cases females lay sterile eggs. One can also modify *selfish genetic elements*, which when released impose a heavy genetic load on the pest. If they can be made to spread, this reduces pest numbers or even causes extinction, the advantage being that far fewer modified insects need be released (Lyttle, 1977; Xi *et al*., 2005). Knipling suggested that, by using an appropriate chemical, pest insects could with advantage be sterilized rather than killed in the field. A further technique is to release insects carrying lethal genes into the pest's population (Yakob *et al*., 2008).

13.2.2.1 Sterile male technique

SMT was developed in the USA (Knipling 1955, 1979; Myers *et al*., 1998) for area-wide eradication of major pests of high-value products, initially of screw worms of range livestock (Section **7.4.1.2**(**d**)). The feasibility of using this method arose when Bushland and Hopkins (1953) showed that these flies could be sterilized by high-energy radiation, but were otherwise unaffected. But the cost is high because large areas are involved and millions of sterile males must be produced, kept alive and then widely released. Some, mainly ecological, features of pests make success more likely: (i) males but not females should be promiscuous, the latter often being so (Song *et al*., 2007); (ii) fertility should be low; (iii) pests should not have huge populations over wide areas as it is necessary to flood them at a ratio of as much as 40:1; (iv) they must be easy to rear, sterilize and conserve in good shape; (v) a high proportion of the wild population should be adult and so long lived; (vi) the pest must not be a long-distance migrant; (vii) the area involved must not be too great for the finance available; and (viii) where a pest is spreading, a pre-emptive strike is best (Knipling, 1955, 1979). Thus, its numbers may be suppressed with a short-term insecticide, improving the ratio of sterile releases to fertile residents.

Irradiation with gamma- or X-rays induces sterility, but the dose and stage at which pests are treated are critical in producing sterile, vigorous males. Exposure must be after gametogenesis. Alternatively, chemo-sterilants may be used but there are greater risks to people and the environment. The mutations induced do not affect the fertilization, but carry dominant lethal genes to the progeny, which die at an early stage (Dent, 2000). In cases in which only the adult is the effective pest, a late-acting lethal gene can be employed. When competition between juveniles is a major factor in natural regulation, this enhances the interaction, killing healthy individuals too. The outcome has been modelled (Yakob *et al*., 2008) in *Aedes aegypti* (Section **7.3.2.4(e)**) for the *RIDL* gene. While concurrent biocontrol with a parasitoid should be favoured at high-to-moderate pest densities, SMT becomes progressively more effective at lower density, leading to eradication (Knipling, 1955; Proverbs, 1969). It is inversely density dependent, but like biocontrol has the advantage of being intrusive.

We already considered a number of cases of SMT. Its first successful use, against screw-worm flies in Curacao (Section **7.4.1.2(d)**), is unsurprising because the island is small. But their eradication from continental USA and Mexico, while much more difficult due to the area involved, shows what can be done with enough political will and finance *if the ecological circumstances permit*. This could be done in Africa for tsetse if discrimination by nubile females against sterile males could be overcome. But the cost would amount to many billions of pounds since the area involved is even larger. For mosquitoes, the technique is inappropriate as they violate almost all the ecological criteria necessary for success (see above). While it has been attempted it has not been effective. Indeed, if high-density larval populations are suppressed, more adults may emerge when intraspecific competition is reduced (Yakob *et al*., 2008). In any case, the field densities of many mosquitoes depend on the number of current breeding sites in the landscape, less so on competition (Section **12.3.4.4(g)**). Combining SMT with classical biocontrol has been suggested for *Anastrepha* (Section **6.3.1.1(l)**), since the former is more appropriate at low pest densities and the latter at high ones (Aluja, 1994). Mating a pest with a close relative can often induce sterility. This has been tried between *Heliothis virescens* (Section **6.2.1.2(h)**) males and *H. subflexa* females. Here sterile males continue to be produced, while females remain potentially fertile.

13.2.2.2 Employing selfish genetic elements

While genetic defects occur in most populations (Enright, 1976), especially when selection has been lax (Ford, 1975), *truly selfish* genes or genetic elements spread in a population despite inflicting a cost to the organism itself, namely, on the rest of the genotype in which they reside (Camacho *et al*., 2000; Trivers, 2008). These elements do not obey Mendelian laws, and by various means spread with increasing frequency. Molecular techniques allow us to transfer selfish genes from other species and to attach deleterious genes to selfish loci. Two such elements are *meiotic drive loci* and *transposable elements* (Hastings, 1994).

It has been known for decades that driving chromosomes exist in some dipteran populations (Hickey and Craig, 1966). In *Aedes aegypti*, a mutant Y-chromosome occurs in some natural populations, which become increasingly male biased and finally extinct, probably in ~15 generations (Hamilton, 1967). Curtis *et al*. (1976) studied this effect in *A. aegypti* in field cages, while Lyttle (1977) did similar work on *Drosophila*. Genomic adjustments, particularly to the nuclear genome, have probably naturally evolved to restrain such a dangerous situation (Charlesworth *et al*., 1993; Burt and Trivers, 2006). But drive leads to the possibility of employing the principle to eradicate mosquitoes as vectors (Curtis, 1992; Alphey *et al*., 2002). Such techniques depend on five factors: (i) the rate of (any) reversion to a non-selfish form; (ii) the evolution of pest suppressor systems; (iii) effects on its fitness; (iv) the mechanism regulating its population size in the field; and (v) the ease of handling the pest in the laboratory (Hastings, 1994). Repeated backcrossing of son-producing males to females of the susceptible population, thus removing any such genomic restraints ((ii) above), may be needed prior to release (Hamilton, 1967). Recent work (Neiman and Taylor, 2009), however, indicates that nuclear and perhaps mitochondrial genomes are well equipped to combat selfish elements. They are not general.

Sex-ratio distorters are naturally of two types, male biasing and female biasing. In the first, apart from Y-chromosome drive above, another type due to B-chromosomes (Camacho *et al*., 2000) is found in a few chalcidoid wasps (*Trichogramma, Nasonia*), in several grasshoppers, and also in some other animals and even plants. Such chromosomes are not found in all individuals within a species and are not essential for their functioning (Perfectti and Werren, 2001). In wasps, they are transmitted via the sperm and strongly bias the sex ratio towards males by condensing the paternal genome but not themselves (Nur *et al*., 1988). Wasps affected become haploid males based on the female's genome. Furthermore, molecular drive within the genome may generate evolutionary novelty, even to the extent of speciation (Dover, 1982).

Driving X-chromosomes occur naturally in some *Drosophila* species (Sturtevant and Dobzhansky, 1936, in Sandler and Novitski, 1957) and meiotic drive has been induced in laboratory house flies (Pedigo, 1996) by sub-lethal irradiation. Recall (Section **9.8**) that *Wolbachia* is a female biasing agent so it might be employed to control mosquito vectors (Xi *et al*., 2005). In such techniques released insects must be in developmental phase with those of the focal population and mix in thoroughly. Jansen *et al*. (2008) have modelled the conditions under which introduced *Wolbachia* would spread in nature. So it might be used to drive deleterious transgenes into a pest population (Benlarbi and Ready, 2003; Sinkins and Godfray, 2004). One would introduce the engineered gene into some individuals and couple it to the maternal transmission of *Wolbachia*. This could be done by integrating the transgene with the *Wolbachia* genome (Turelli and Hoffmann, 1999).

Unfortunately, an excess of males can also occur in Ichneumonoidea cultured for biocontrol (Stouthamer *et al*., 1992). It results from there being two genetic male forms: diploids, the result of a sex-determining mechanism at a single locus, and normal haploids. Such an excess reduces the effectiveness of these agents in the field. Diverse mechanisms determining sex have long been known in the Hymenoptera (Flanders, 1945).

Genetic modification is a potentially effective means of controlling pests. Recall (Section **12.3.4.4**(e)) that closely related species, which presumably differ in only a few genes, may be very different in commonness and rarity. Now, transposable elements are special genes that have the capacity to make extra, non-Mendelian copies of themselves and place these elsewhere in the genome (Trivers, 2008). Thus, a genome may become rich in these elements, although the rest of the genome inactivates many of them. Furthermore, conditional lethal mutations can be introduced into a pest's population. A main research area here in temperate species seeks to abolish their cold hardiness, an attribute linked to diapause (Section **10.2.3.3**). In widespread species, such as *Ostrinia nubilalis*, releasing 'non-diapausing' genotypes from south to north results in considerable winter mortality (Pedigo, 1996). The method might be used in other widespread pests, although one must recognize the risk of enhancing their genetic diversity and thus increasing their adaptability. Also, one wonders how maladapted genotypes could spread in populations (Section **9.10**), repeated releases would be necessary.

13.2.3 Environmental methods: Chemical and physical

13.2.3.1 General introduction

Great efforts, especially during the past 70 years (Casida and Quistad, 1998; Oerke, 2006), have been directed towards improving all practical means of pest control by modifying the environment external to the pest, but especially by applying new insecticides. In the early days, the sudden efficacy of chlorinated hydrocarbons such as DDT, BHC and aldrin led chemists and farmers to believe that salvation was at hand. To save time and costs there were, as we noted, lapses from existing cultural practices. But the more tangible forces of natural selection were also at hand, as H.S. Smith pointed out as early as 1941, and resistant strains of pests evolved. Their rapid development is a stunning case of evolutionary speed in insects. Thus, house flies became resistant to DDT by 1948 and Colorado beetles to it not long after. Georghiou (1986) found >500 cases of insects evolving resistance to insecticides. But by no means all such pests have developed this ability.

Unfortunately, insecticides may kill a pest's enemies preferentially, although with a little knowledge this can be reduced or avoided. But insecticides, as well as herbicides and fungicides, can have further bad effects in weakening the natural resistance of crop plants (Wu *et al*., 2001, 2004). This often results from sprayed plants having reduced photosynthetic rates, since the chloroplasts may be damaged and/or the biochemical pathways upset (Murthy, 1983). Ultimately, the plant's induced resistance (Section **2.4.2**) is reduced. But broad beans attacked by *Aphis fabae* and treated with the pyrethroid 'Cymbush', showed not only increased growth but so did the aphids (Hutt *et al*., 1994)! The effect was not due to its active ingredient, cypermethrin, but to the emulsifier commonly present in such preparations. Note that commercial insecticides have an abbreviated chemical name and a trade name for its formulation, thus 'carbaryl' may be marketed as 'Sevin', adding more confusion.

13.2.3.2 Organic pesticides in the arsenal

Insecticides can be classified under two headings: their *chemical class* and their *route to the insect*. The former contains organochlorines (OCs), organophosphates (OPs), carbamates, synthetic pyrethoids, avermectins, formamidines and nicotinoids. The latter includes ephemeral contact, residual contact, stomach, trans-laminar, systemic, quasi-systemic and fumigant poisons (Table 13.1). Over the last 60 years, pesticides of increasing toxicity to insects and decreasing toxicity to mammals have been synthesized. Thacker (2002, see Fig. 1.3), in an insightful graph, shows how application rates have greatly diminished during this period.

With the advent of DDT, other long-life OCs, such as γ-BHC (= lindane, = HCH), and the cyclodiene group (dieldrin, endrin, aldrin and endosulfan), were quickly developed, displacing heavy-metal poisons and becoming dominant in the 1950s. All are broad-spectrum neurotoxins and kill most insects, while the cyclodienes are also toxic to mammals. Although many are banned in several countries, elsewhere some are still used today, a convenient and profitable dumping ground! But DDT remains an excellent house spray against anopheline mosquitoes. It is cheap, has good residual action and low mammalian toxicity. When its use was discontinued in KwaZulu-Natal, South Africa, malarial cases increased about tenfold within a few years (Thacker, 2002). The drawbacks of OCs are well known: they have high field persistence leading to various long-term pollutions. Their continued use on cane and bananas in Australia into the 1980s led to contamination of beef for export (Walter, 2003). They accumulate in vertebrate body fat becoming increasingly concentrated as they pass up the food chain. This *biomagnification* may be of the order of a million times their initial concentration.

Organophosphates have been produced from the late 1940s and were developed from research into nerve gases during WWII. Again, they are neurotoxins and work by inhibiting the action of the enzyme acetylcholinesterase (AChE), which is responsible for the breakdown of the neurotransmitter acetylcholine (Thacker, 2002). Unsurprisingly, they are very toxic to people and other mammals alike, which is because they all affect the same

Table 13.1. Chemical class and mode of action of some well-known insecticides.

Mode of action	OC	OP	Carbamates	Pyrethroids	Avermectins	Amidines	Nicotinoids
Ephemeral contact		Malathion	Pirimicarb				
Residual contact	DDT HCH Endosulfan Chlordane	Dieldrin* Endrin* Chlorpyrifos Diazinon	Carbaryl Methomyl	Cypermethrin Deltamethrin Permethrin	Ivermectin Allethrin Cyhalothrin	Amitraz Chlordimeform	Imidacloprid
Stomach poisons	DDT HCH Endosulfan Chlordane	Dieldrin* Temephos Parathion Endrin* Trichlorfon	Aldicarb Carbaryl Carbofuran Furathiocarb	Deltamethrin	Allethrin		Imidacloprid
Systemic poisons		Metasystox Disulfoton Phorate	Carbofuran Aldicarb Pirimicarb Furathiocarb Methomyl				Imidacloprid
Quasi-systemic poisons		Dimethoate					
Fumigants		Malathion	Methomyl Pirimicarb				

OC, organochlorine; OP, organophosphate. Amidines include formamidines. Several compounds have more than one mode of action and some (*) are no longer manufactured.

enzyme. But they are still the largest group of insecticides in current use, having the merit of a rapid breakdown in the field, which leads to fewer problems than with OCs. They are all based on phosphoric acid and come in three chemical groups: (i) aliphatics such as TEPP, malathion, dimethoate, disulfoton and trichlorophon; (ii) phenyl derivatives such as ethyl and methyl parathion, fenthion (= Baytex) and fenitrothion; and (iii) heterocyclic derivatives such as diazinon, phosmet, chlorpyrifos and fonofos.

Generally, aliphatics have the shortest life in the field, that for TEPP is only 12–24 hours, while heterocylics have the longest life. The acute mammalian toxicity of parathion prohibits its general use. After widespread application of relatively innocuous DDT, there were many cases of toxic effects to operators by OPs. A survey in the Philippines (Teng, 1994) showed an increase in human deaths of 27% where these insecticides had been misused. Conversely, the very short half-life and fumigant action of malathion is useful when a quick kill of a pest is needed just before crop pollination or harvesting. It has been used for over 50 years and is one of the safest insecticides. Trichlorfon, although toxic to many pest species, particularly dipterans, has a lesser effect on some of their natural enemies, and thus may tip the balance of pest numbers favourably.

Some of these insecticides are *systemic,* they are translocated with variable efficiency through the plant's vascular pathways, especially xylem. Dimethoate is partly and metasystox and disulfoton are fully systemic. They move to the growing points, where aphids and other piercing and sucking pests extract them from the vessels, much to their detriment. Such a property means that beneficial insects visiting the crop after spraying, and merely walking over the plant surface, are little affected. Even so, honey bees are harmed by dimethoate (Potts, 1990). Systemics can be absorbed from the soil, or sprayed on just a part of the plant, so conserving some of the natural enemy force, which can spread subsequently. Of course, insecticides should hit the pest as hard as possible and its enemies as little as possible.

Carbamates, based on carbamic acid, were introduced in 1956 with the development of carbaryl, which has been used widely against caterpillars and other foliar pests. Like OPs, they are AChE inhibitors. They come in three chemically distinct groups. Carbocyclic carbamates include carbaryl, propoxur and methiocarb, heterocyclic carbamates include carbofuran and pirimicarb, while aliphatic forms, all of which are systemic, are aldicarb, aldoxycarb, methomyl and oxamyl (Thacker, 2002). Carbamates, often called methyl-carbamates (MCs), usually have a persistence and toxicity intermediate between OCs and OPs, but many are very toxic to bees and parasitic wasps. Aldicarb and carbofuran are persistent, but their usefulness is limited by their high mammalian toxicity, in the former being ~1 mg/kg. Again this is due to their blocking the action of AChE. Aphox (= pirimicarb) has interesting properties: it is a fumigant, a systemic and has rather low toxicity to mammals, bees, parasitic wasps and carabid beetles. In *Pterostichus cupreus* fed on aphids contaminated with aphox, the fat bodies were absent but the rate of egg laying accelerated (Wallin *et al*., 1992). While non-persistent it is deadly against dipterans and kills aphids. In addition to their insecticidal properties some carbamates act as *antifeedants*, namely they stop pests feeding without repelling them.

The formamidines, including chlordimeform and amitraz, have found a commercial niche recently where resistance to conventional insecticides has evolved, because they block neural transmission differently. Chlorantraniliprole upsets the insect's calcium metabolism, stops eating and so kills it. It works well against lepidopteran pests, but some, including *Plutella xylostella*, have become resistant to it (Ribeiro *et al*., 2014).

The relative success of natural pyrethrum, which occurs in the petals of *Chrysanthemum* species grown in Kenya and other places, attracted the attention of chemists late in the 1940s. The logic of choice was that if these plants had been combating insect attack for aeons, synthetic derivatives of their secondary compounds might be less prone to induce insect resistance. They have a different action on the insect's nervous system than OPs and MCs, since they block the voltage-dependent sodium channel (Casida and Quistad, 1998). Much development of this group took place at Rothamsted Experimental Station, UK, under M. Elliott. Natural pyrethrum is a mixture of pyrethrin 1 and 2 and cinerin 1 and 2. In 1949, allethrin was synthesized and duplicates the activity of cinerin 1. Since then pyrethroid chemistry has been much developed. In the 1970s, molecular permutations produced really successful insecticides, a process continuing today. Synthetic pyrethroids offer three advantages over natural pyrethrin: greater photostability, higher toxicity to insects and cheapness. Permethrin was introduced in 1973 and has an application rate of only ~100 g/ha, while fourth-generation compounds (cypermethrin, deltamethrin) can be used at even lower rates and have greater toxicity. Cypermethrin is ~300 times more toxic to many insects than DDT and has only 60% of its human toxicity (van Emden and Service, 2004). Unfortunately, it kills all natural enemies, as is often the case with insecticides, be they predatory beetles or parasitic wasps. Even so, these compounds do have some repellent effect and if sprayed in the field on a sluggish pest with mobile enemies, some effective selectivity ensues. While they interfere with neural transmission and are either stomach or residual contact poisons, they are not systemic.

Other insecticidal secondary compounds from plants are rotenone (from roots of the legumes *Derris* and *Lonchocarpus*), ryania (from *Ryania*, Flacourtiaceae), azadirachtin (from neem trees, *Azadirachta indica*, Meliaceae) and nicotine (from tobacco, *Nicotiana*, Solanaceae). These have not led to the development of synthetic derivatives to the extent pyrethrum has, although imidacloprid is a successful new nicotinoid and others like acetamiprid and dinotefuran have been registered. But using imidacloprid to control scale insects on Californian citrus has been found to compromise IPM (Section **13.3**), while resistance to it has developed in *Nilaparvata* (Matsumoto *et al.*, 2013; Section **5.3.1.2(d)**). Neem extracts show promise against various pests (Casida and Quistad, 1998) and have antifeedant and repellent properties. Having read Section **2.4.2** we are unsurprised that many other plants contain substances with insecticidal properties so being a rich source of potential new ones. Over 3000 alkaloids have thus been identified (Thacker, 2002). Antifeedant and insecticidal activity occurs in seed extracts from trees in the Annonaceae and Meliaceae (Leatemia and Isman, 2004).

In 1911 the German bacteriologist Berliner described *Bacillus thuringiensis* (*Bt*) from infected pupae of *Ephestia kuehniella* (Section **6.3.1.2(q)**) in a grain store at Thuringen. It is now a most effective weapon against endopterygote pests. Poisons like *Bt* toxin, prepared from this bacillus, or spinosad, from a soil actinomycete, are logically similar to pyrethrum or rotenone extracted from flowering plants and best labelled *microbial insecticides* (Stern *et al.*, 1959). The *direct use* of micro-organisms is considered in Section **13.2.4.5**. The crystal toxins *B. thuringiensis* produces (δ-endotoxins or Cry proteins) are used either directly, or more often in transgenic crops. When susceptible insects, such as caterpillars and plant-eating beetles, ingest them these toxins are proteolytically activated in the midgut, bind to membrane receptors, leading to pore formation, septicaemia and death (Tabashnik, 1994; Griffitts *et al.*, 2001). Several strains of *B. thuringiensis* exist, each producing a set of Cry proteins. These strains are *Bt* var. *aizawai* (*Bta*), *Bt* var. *entomocidus* (*Bte*), *Bt* var. *israelensis* (*Bti*), *Bt* var. *kurstaki* (*Btk*), *Bt* var. *tenebrionis* (*Btn*) and *Bt* var. *thuringiensis* (*Btt*). *Bt* δ-endotoxins include Cry1Ac, Cry2A, Cry5A, Cry14A and many more. Cry1 and Cry2 are toxic to Lepidoptera, Cry2A to Diptera such as larval mosquitoes and black flies. Useful as these toxins are, some insects are developing resistance to them (Tabashnik, 1994; Gassmann *et al.*, 2009; Section **13.2.3.4**). In addition, the bacterium *Photorhabdus luminescens*, a symbiont within entomopathogenic nematodes (Section **13.2.4.5**), possesses a high molecular weight protein that is very toxic to insects (Bowen *et al.*, 1998).

The avermectins were produced originally by fermentation from *Streptomyces avermitilis* mycelium and have been used from the late 1980s. They are valuable in having anti-helminthic as well as insecticidal properties and low mammalian toxicity. Ivermectin is crucial in the war against filarial worms causing elephantiasis (Section **7.3.2.4(g)**) and river blindness (Section **7.3.2.4(i)**). Abamectin is used on pest caterpillars that have become resistant to older insecticides. Lately, spinosad, a mixture of spinosyn A and spinosyn D, which are tetracyclic macrolide neurotoxins produced by fermentation of the soil actinomycete *Saccharopolyspora spinosa*, is highly toxic to a range of Diptera and Lepidoptera (Bond *et al.*, 2004). It has low mammalian toxicity and is both a contact and stomach poison, being effective against many field and orchard pests. Dust formulations of it may become useful to suppress beetles in stored products (Nikpay, 2007). Even so, resistant strains to it have developed in *Plutella xylostella*, *Heliothis virescens* and *Musca domestica* (Li *et al.*, 2007).

The concept of synthesizing mimics of insect growth hormones (IGRs) again dates from the early years after DDT, although some plants had already developed this idea (Section **2.4.2**). IGRs are rather non-specific within juvenile insects, and are unlikely to affect non-arthropods. Nor do they trouble adult insects and hence are to an extent 'friendly' to many insectan enemies of insects. Naturally, if the numbers of a pest are greatly reduced, those of its specific enemies will be too (Section **12.3.4.4**). But while useful, these mimics have not become the panacea predicted, partly because of their high cost but also because of the surprising development of resistance to them, as in larval *Aedes* to the juvenile hormone (JH) analogue methoprene. But they are very effective against fleas, and diflubenzuron, a chitin synthesis inhibitor, suppresses caterpillars and whiteflies (van Emden and Service, 2004). Cyromazine is useful against *Delia antiqua* (Section **3.2.1.2(g)**). In European IPM apple orchards, fenoxycarb, another JH analogue, is applied regularly to suppress the tortricid complex, including the ubiquitous *Cydia pomonella* (Section **6.3.1.1(g)**). Pyriproxfen and buprofezin have been used experimentally on Californian citrus (Grafton-Cardwell *et al*., 2006) and on Australian cotton (Grundy, 2007). Dimilin and triflumeron interfere with the maturation of nymphal locusts (Lomer *et al*., 2001).

13.2.3.3 Formulation and application: How to deliver

The effective use of insecticides involves two questions. (i) How is a specific application expected to impact the population dynamics of the pest? (ii) What is the relationship between loss of yield caused by the level of infestation and the total cost of using the insecticide (Dent, 2000)? One must also use effective delivery techniques. Chemicals should be applied only when all else fails, while timing is often a critical part of their effectiveness. But we have a long way to go, especially with implementation. While insecticides are very poisonous to insects, the problem is getting them onto or inside the brutes. Insects may eat them with their food or absorb them through their cuticle and fumigants enter their spiracles. Some modern pyrethroids are required at only 10 g/ha, so great dilution is necessary. Formulation is a critical part of the *delivery system* of insecticide to insect. We consider it here only briefly; not as technology but more as environmental physics.

Insecticides are usually applied as liquids that evaporate to give a toxic film. They are not often sold pure, but are mixed with other chemicals, both to improve shelf life and, like wetters and stickers, to maximize effectiveness. They come as emulsions or powders to be mixed with water in various proportions, producing either *high volume* or *low volume* sprays. The former are diluted at rates of ~200–500 to 1. Formulations may also be applied dry as dusts or granules, the difference here being one of particle size. Baits contain ~5% active ingredient plus a substance attractive to the pest insect. For practical details see Matthews (2000).

So formulation and application are inseparable. For foliar sprays there is an optimum size range for the droplets, often ~100–150 μm, although this range varies depending on the nature of the foliage. Larger drops are thrown farther but tend to run off and soak the ground beneath, whereas smaller ones, while potentially giving better coverage, tend to drift off in even a light breeze to pollute adjacent crops or the landscape in general. In California, increasing attention is being paid to aerial pollution by insecticides and other agro-chemicals (Trumble *et al*., 1997). In this context, wettable powders lacking volatile solvents are less offensive. But in all, only 1–5% of the spray sticks to the plant, an appalling waste, but the alternative is to paint each leaf or fruit with a brush! Then the amount that actually kills the pests is only a minute fraction of this! Some systemics, however, can be absorbed by roots and usefully translocated. In spraying fruit or foliage, *phytotoxicity* is a further important consideration (Murthy, 1983; Wu *et al*., 2004).

Traditional spraying equipment gave poor control of droplet size, with the majority of the liquid forming drops that were either too large or too small. More recently, *spinning cage* and *spinning cup* spray heads have been developed. These give a narrower and more controllable spectrum of droplet size, one appropriate to the case in hand. Even so, a definable *range* of sizes is required for any combination of weather and crop; there is not one universal, optimal size for droplets. Electrostatic sprayers, which impart a charge to the droplets attracting them to the foliage and minimizing wastage, have been built and marketed. One of their problems is that droplets are attracted to peripheral foliage and hence do not penetrate the plant. This line of development has recently been abandoned (van Emden, personal communication). For small-scale application the twin spinning disc knapsack sprayer, introduced about 1990, is more efficient than earlier equipment.

Dusts have the advantages of not requiring water or complex equipment for their application: often a nylon stocking is all that is needed at the small-scale level. Early morning is the best time for application, when dusts adhere to the dewy foliage. This simplicity is a great advantage in developing nations where water may be short and mechanical spares and know-how shorter. It is common to see expensive machinery rotting away for lack of these essentials. Personal contamination is a persistent problem, one exacerbated by previous experience with benign DDT. Insecticides with a high mammalian toxicity should be sold to and used only by professionals. In Jamaica, I have seen insecticides stored in unlabelled soda bottles in domestic kitchens!

According to when applied, insecticides can act either as density-dependent or density-independent mortality factors (Section **10.2.1**). If they are applied only when pests are above the EIL they will be the former, but if as an insurance they will be the latter. Also, formulation can be used to effect selectivity of action on pests and their enemies (Section **13.3**) and hence be an important part of IPM. Indeed, although IPM emphasizes the reduction in use of traditional insecticides, these will probably always be useful as they give an immediate kill in an emergency.

13.2.3.4 Insect resistance to insecticides

An odd fact about resistance is that it varies greatly, even among unexposed insects. Thus, in the 1950s some unsprayed strains of Sitona lineata weevils had >30 times the resistance to DDT when tested compared to others. But many pests never develop insecticidal resistance at all (Blows and Hoffmann, 2005), probably because they lack appropriate genetic structures (Bradshaw, 1991). Resistance is due normally to variation in physiological processes or behaviours that do have a genetic basis. Heritable variation is the basis of natural selection (Section **9.1**). Of course, pesticides do not induce resistance directly, they provide selection for an ability to survive the chemical used, so promoting evolution of resistance in the exposed population. But careful as one might be to apply the right spray at the right time, some individuals inevitably survive, carrying their survival strategy to future generations. To date, >600 insect species, ~30% of well-known pests, are resistant to some or other insecticide. Hemipteran, coleopteran and lepidopteran pests are especially prone to develop this ability (Roush and Tabashnik, 1990). Again, taxonomy gives clues about biological processes. One reason why many insects can detoxify insecticides is that the latter are biochemically similar to toxic secondary compounds produced by plants in their own defence, a defence that insects have already breached in the past.

Variable resistance provides a spectacular amount of raw material upon which natural selection acts. Before Ford and Kettlewell's work (Ford, 1975) selective advantages were thought, erroneously, to be of the order of a few per cent (Haldane, 1932). But they are often much greater. Kettlewell investigated peppered moths in their natural, unpolluted environment, and found that normal moths had a sixfold advantage over melanic ones, the latter having previously adapted to industrial areas. In glasshouses Myzus persicae can show a 4000-fold resistance to OPs (van Emden and Service, 2004), an extreme example both of insect adaptability and the driving force of natural selection. Apart from genetics, high turnover of population and multivoltinism (Section **13.1.2.1**) are features favouring the rapid development of resistance. Thus multivoltine tropical pests tend to become resistant faster than temperate ones (Thacker, 2002, p. 95). If an increasing number of annual applications are given to a crop this also drives resistance. Unsurprisingly, several cotton pests, being multivoltine and subjected to many annual sprays in warm environments, have become hugely resistant. Ultimately, repeated spraying is uneconomical and the crop cannot be grown solely under chemical control, a situation often forcing the adoption of IPM (Section **13.3**). Growers are brought, kicking and struggling, into the twenty-first century. And recall too that several insects are pests as a result of spraying.

Another feature is cross resistance, the ability of insects to detoxify an insecticide to which it has been exposed, confers enhanced resistance to others to which it has not. Such resistance is likely when the action of the insecticides involved has a similar effect on pest physiology, as with OPs and carbamates blocking AChE. Multiple resistance is simply resistance to two or more pesticides to which they have been exposed. When pests become resistant to an insecticide, a number of options are open, which can be called resistance management. The traditional approach was to 'up the ante': increase application rates and concentrations to destroy the resistant genotypes before moving to a different insecticide. This has been used with some pest mites. But increasing use of such chemicals may be debarred with food crops, and environmental pollution often ensues. Then one may use a rotational pattern of several appropriate insecticides at normal levels. Also, moderation of use and better timing can be tried, thus allowing natural enemies to resurge, an approach in the direction of IPM. Recently, the development of Bt endotoxins (Section **13.2.3.2**) often provides a better solution.

In about 1985 two moths developed strains resistant even to *Bt* (Gould, 1998). In the diamondback moth resistance is now geographically widespread, no doubt due to its great powers of redistribution. In Indian meal moths one strain has ~100-fold more resistance than normal moths. In *Heliothis virescens* >1000-fold resistance to *Btk* occurs (Tabashnik, 1994). In *P. xylostella* a new gene gives resistance to four *Bt* toxins (Tabashnik *et al.*, 1997). Similar studies with *Aedes aegypti* and *Culex quinquefasciatus*, however, produced no such dramatic results. A resistant strain of *Trichoplusia ni* also survives low winter temperature better, there is no trade-off (Caron and Myers, 2008)! In *Heliothis* and *Plutella* cross resistance to some Cry proteins occurs, but in many species it does not. So the development of *Bt* cultivars with two or more distinct Cry proteins, namely the ones to which cross resistance is not expected, should delay the evolution of resistance, especially if deployed within a mosaic of cultivars (Ives, 1996; Gassmann *et al.*, 2009; Section **13.1.2.2**).

When spraying stops, any genes coding for insecticidal resistance *lose their advantage*. But the physical environment may play a role (Section **10.2.1**). In China, Li *et al.* (2007), assessing the RS of a *P. xylostella* strain resistant to spinosad, found that while there was only a small reduction at normal field temperatures, at low and high fluctuating temperatures RS was greatly reduced. Strains of this moth resistant to chlorantraniliprole have small mature larvae and low growth rates, as do those of *Spodoptera exigua* (Ribeiro *et al.*, 2014). Fitness costs of resistant strains at low temperatures are known in *Culex pipiens*, *Musca domestica* and *Leptinotarsa decemlineata* (refs. in Li *et al.*, 2007). But note above the special case of *T. ni*. Our increasing general knowledge of the vulnerability of resistant strains will be useful in improving control methods.

Perlak *et al.* (1991, in Gould, 1998) were able to effect specific alterations in plants to the DNA sequence of *Bt* toxin genes, resulting in a dramatic increase in toxin production. But the identity of genes in insects that confer resistance to *Bt* has proven enigmatic, although a major one is an autosomal mutant (Ferre and van Rie, 2002). The mutant is prone to be lost, probably due to fitness costs in the absence of *Bt* (above), suggesting that many resistant strains of insects, as above, will have reduced RS compared to wild type. This agreeable idea is supported by the low allelic frequency of genes conferring resistance in natural populations, a feature that also delays the rise of strains resistant to traditional insecticides. Reduced RS in such strains is also known in *Myzus persicae, Lucilia* and *Pectinophora* (Caron and Myers, 2008). Physiological resistance is often based on a single, mutant gene. When its selective advantage is high, it spreads rapidly. While polygenic resistance is known, it is over-shadowed in field populations by the effects of single major genes (Dent, 2000). Phenotypic mechanisms are multiple. They may involve a thicker and less permeable cuticle, increased levels of detoxifying enzymes, storage in fat, reduced sensitivity at the target sites and faster excretion. Once more, *resistance to insecticides often disappears in their absence* (Section **13.2.3.2**).

13.2.3.5 Largely physical and mechanical methods

Mechanical factors have been poorly studied in insect ecology (Section **10.2.3.6**). But they form a diverse and important facet in the control of our insectan enemies, first by intercepting them when they are seeking our crops, stored products, livestock and ourselves (Section **10.2.4.5**), and second as a direct means of destruction. In addition, manipulating these factors can make pests more vulnerable to their enemies. Both passive and active physical treatments can provide a cost-effective supplement to other more sophisticated areas of IPM (Vincent *et al.*, 2003). These methods are particularly suited to post-harvest situations in which the pest has been concentrated along with the crop and where chemical contamination must be avoided.

13.2.3.5(a) TILLAGE. Tillage started with hand-held tools: forks, spades and mattocks, hoes and machetes for the surface work. At this personal scale one can kill pests as they are uncovered and recognized. Mechanical power allowed the use of new implements: steel ploughs, tines, harrows, disks and rollers. Early tractors were so small that you could literally throw your leg over them to start, now some are ~4 m tall with cabs insulated from the outside world. Like a facet of the history of warfare, you get farther and farther away from your enemies until you cannot even see them. Tillage is primarily for weed control, incorporating organic matter in the soil, allowing water to penetrate and producing a suitable seedbed, so enhancing crop growth, but it may kill pests as well. Fat and squashy soil insects, like scarabaeid grubs, and those that build silk structures before pupation, like swift moth larvae and some other moths, are vulnerable to mechanical damage or deep burial from tillage. The type of plough used is influential (Dent, 2000). Tillage dries the soil and desiccates pest pupae or egg pods of pest grasshoppers. Heavy rolling restricts movement of mobile stages. In areas prone to erosion, *conservation tillage*, in which there is minimal soil disturbance (Stinner and House, 1990), may be the best policy and can limit populations of *Diabrotica* beetles (Section **3.2.2.1(a)**). Minimum tillage ('mintil'; Fig. 13.2), which is now practised on ~30% of the crop area in the UK (O'Brien *et al*., 2008), also requires less work, with attendant savings in time, machine parts, fuel (up to 60% less), and so CO_2 emission.

13.2.3.5(b) IRRIGATION. Crop growth is often improved by irrigation. When there is inadequate rainfall it sustains agro-ecosystems, and is crucial in climates where evaporative rates are high. Again, there may be effective spin-offs for pest control. First, its mechanical action may wash off small insects such as aphids or trap them in surface films (Section **1.2**). In flooded paddies some pests fall into the water and drown and pests in the soil are destroyed. In China, deliberate alternate flooding and drying out of rice paddies conserves water and reduces mosquito numbers (*Anopheles sinensis*, *Culex tritaeniorhynchus*; Sections **7.3.2.4(d)** and **7.3.2.4(f)**), by deterring oviposition and desiccating juveniles. Second, biological interactions may be promoted. Physically stressed plants often have

Fig. 13.2. Minimum tillage, 'mintil' in operation. The method saves much fuel over traditional deep ploughing.

increased levels of free amino acids (White, 1993; Section **10.2.2.5**), promoting improved RS of pests, so irrigation reduces this effect. In permanently flooded paddies ducks and carp eat mosquitoes, fertilize the rice with their faeces and provide an additional crop (Section **13.3.2.2**). Flooding is used in growing cranberries and in spring kills the cranberry fruit worm *Acrobasis vaccinii* (Pyralidae). In vineyards it destroys grape phylloxera (Section **5.3.1.2(g)**) but can be used only on level or terraced ground. Overhead irrigation may interfere with a pest's various activities, especially mating and oviposition. It has been used in orchards against codling moths and in field crops against diamond-back moths. Mulching can be considered here since it retains moisture. It provides a refuge for predators of Colorado beetles, gives higher yields of potatoes (Brust, 1994) and can be effective in other crops.

13.2.3.5(c) EXCLUSION. Stemming from the fact that insects show appetitive movement in search of resources, pests may be partially or totally intercepted while in this behavioural phase (Section **13.1.3**). Stored-products pests (Section **6.3.1.2**) can be totally excluded by appropriate packaging or within buildings and silos. For endophilic biting flies, screening doors and windows with plastic (temporary and cheap) or stainless steel mesh (permanent and expensive) will exclude them. Bed nets are a cheap solution too, a means advocated by Sir Ronald Ross over a century ago (Section **7.3.4.2(d)**). When impregnated with a synthetic pyrethroid they can be practical and effective. A continuing programme in Kenya is projected to halve the incidence of malaria. Screens can partially exclude flies from stables and abattoirs. Pit latrines, which *Culex quinquefasciatus* (Section **7.3.2.4(g)**) favours for breeding, can be given a snowy topping of polystyrene beads, which prevents both oviposition and emergence.

Partial exclusion can be achieved for some field crops with mesh fences to intercept low-level migrants: one at 1 m high excludes 80% of *Delia radicum* (Vincent *et al*., 2003; Section **3.2.2.1(i)**). A similar trap of biological origin is a tall crop at the periphery of the field (see Sections **13.2.3.5(d)** and **13.2.4.4**). In horticulture, split tar-paper discs may be placed around young brassica plants to stop egg laying by *D. radicum*. With respect to insect vision, materials that reflect ultraviolet light, such as aluminium foil, polyethylene and mica, placed in a field crop (Fig. 13.3), repel questing thrips and homopteroids (Kring, 1972; Prokopy and Owens, 1983).

13.2.3.5(d) TRAPS. Traps are different from exclusion systems in that they retain pests, which then may be destroyed, or in the case of organic mulches, returned to the soil as fertilizer. Recall that traps usually depend on the pest's appetitive movement. They often exploit either its vision or its olfaction. Here we consider only constructed traps; biological trap crops (Section **13.2.4.4**) partly exclude and partly retain pests and have other effects. On the ground, trenches both exclude and trap walking pests such as chinch bugs. In a North American trial, a 25 cm V-shaped trench lined with plastic retained 95% of adult Colorado beetles. Some, like those used to capture tsetse, work because they interfere with the insect's behavioural sequencing. Many traps have been used in homes: from sticky fly papers displaying the cadavers for all to view, to discretely placed cockroach traps that have adhesive floors or poisoned baits. In glasshouses, coloured sticky traps depend upon the fact that certain pests are attracted to specific wavelengths (Briscoe and Chittka, 2001), while their insectan enemies are not. Such traps operate as an additional predator, further tipping the balance in the grower's favour.

While improvements are being made, traps often do not reduce a pest's population significantly except, as in tsetse, where its reproductive rate is low (Section **7.3.2.4(m)** and Fig. 13.4). But it does occur where the traps themselves are efficient, as for boll weevils (Section **6.2.1.2(c)**), in which an estimated 76% of the overwintering population has been captured (Smith, 1998). Here, a mimic of the pheromone emitted by males (Grandlure) attracts both sexes, which die in contact with malathion. Improvements in codling moth traps (Witzgall *et al*., 2008) have been made. The invasive moth, *Teia anartoides*, is being eradicated from Auckland using pheromone traps baited with irradiated virgin females (Suckling *et al*., 2006). Traps are often used in research (Taylor, 1986; Southwood and Henderson, 2000), the aim being to get representative samples. They are also valuable in assessing the need to spray and to improve timing in IPM strategy (Whalon and Croft, 1984; van Emden and Service, 2004). They allow action to be organized in advance and reduce the amount of insecticide applied. But the basic problem is deciding what a

Fig. 13.3. A reflective mulch used on a horticultural scale. Source: Wikimedia Commons, credit to Jonathan Billinger.

given catch means in relation to real pest density. Analyses show that at least 30 traps must be used to make acceptably accurate estimates (based on the binomial distribution of traps with and without captures) and hence decisions (Nansen *et al*., 2008).

Specific pheromones may be used in two ways: (i) to attract a pest species to a point source, the trap, wherein it is destroyed; or (ii) to disrupt mating, when they are generally distributed in small dispensers in the crop, orchard or forest making it difficult for males to find females. Their use represents an alteration of the intraspecific environment. They are often used on high-value crops (Cardé and Minks, 1995) such as cotton and orchards. But application on a wider scale, for example, against forest pests such as spruce budmoths (Rhainds *et al*., 2012), is being researched. When traps are used without insecticides, natural enemies may survive better and their numbers resurge, placing the pest between a rock and a hard place.

Pheromones are often highly specific and even vary geographically within the range of a species. Not all insects, however, produce the *long-range* pheromones that must be present if baiting is to be effective. While trapping only females would be best, unfortunately it is usually females that produce the pheromones, so catching ardent males. But even if 90% of males were so destroyed, in long-lived species it would likely have little effect on fertility, due to their general promiscuity and the promiscuous behaviour of females (see Song *et al*., 2007). We also recall (Sections **9.1** and **9.6**) that while a secondary sex ratio with a high proportion of females would be *good for a species*, evolutionary imperatives usually favour selection at the *individual level*, thereby giving equal investment in the two sexes (Fisher, 1930; Hamilton, 1967). Even so, if short-lived females have to wait longer to get mated their AF may be reduced, and a Williams' effect could become significant.

Fig. 13.4. The effective bi-conical trap for tsetse being set up in East Africa. Their slow reproductive rate makes them vulnerable to such methods of population reduction. Source: Flickr, credit to Peter Rickwood/IAEA.

Mating disruption involves several mechanisms: (i) it could result from over-stimulation or physiological imbalance of the sex pheromone receptors in males; (ii) a high level background of synthetic pheromone may camouflage natural emissions from females; or (iii) it may result in males following false trails, which of course occurs when they are trapped (Rhainds *et al.*, 2012) and in which case density effects may be important. While these pheromones occur widely in the Lepidoptera (Cardé and Minks, 1995), they are sporadic in the Diptera, being absent in tsetse but present in *Contarinia* midges and house flies. Aggregation pheromones, to which both sexes respond, are found in some Coleoptera, and are well studied in bark beetles (Section **4.2.1.2(h)**). They may also attract specific enemies, in this case *Rhizophagus* and *Thanasimus* beetles (Section **9.8**). Their use in 'trapping out' boll weevils has been effective. Traps placed in the lea of vegetation generally catch the highest numbers. For *Hypothenemus hampei,* pheromones have been used in traps but an ethylene/methylene mixture is more effective and best used to attract these sneaky beetles *away* from the crop (Fig. 13.5). The anti-aggregation pheromone MCH repels Douglas fir beetles. For cost effectiveness, spacing of the dispensers and the concentrations they emit, must be optimized (Ross and Wallin, 2008). Pheromones exist in cockroaches but operate as tactile messages, as would be expected from the cryptic lifestyles of these revolting beasts.

Using the fact that blister beetles attacking millet are attracted to light, some West African farmers set night fires to attract and destroy such insects (Abate *et al.*, 2000). Ugandans have long used this method to catch grasshoppers ('essenene'), which they steam and fry as human food.

Fig. 13.5. Winston Shaw, a Jamaican coffee farmer, with an effective ethylene/methylene trap (made from a discarded soda bottle!) for coffee berry borers. With a little encouragement local farmers can develop cheap, practical methods themselves.

13.2.3.5(e) TEMPERATURE. Because insects have upper and lower lethal zones, extremes of either high or low temperature may be used to kill pests after harvest. Storing fruits and vegetables just above zero extends their shelf life and kills most pests (Neven, 2004). Hot water and hot air treatments are used to quarantine fruits: mangoes are routinely immersed in water at around 50°C, but temperate fruits are damaged more easily. Covering many biological materials with black plastic will often raise the temperature beneath it sufficiently to kill insects.

13.2.3.5(f) INORGANIC DUSTS. We noted in Section **13.1.3** that a traditional African method against pests in stored grain is to use fine dusts. These abrade the cuticle and cause desiccation. Kalmus (1944), after a suggestion by Wigglesworth, showed that *Drosophila* spp. were killed rapidly at 40–50% relative humidity by charcoal dust. Developments under the high-sounding term '*particle film technology*' show promise in the control of diverse pests, both in the field and in storage (Vincent *et al*., 2003), and may even improve crop growth (Lapointe *et al*., 2006). Inert dusts include lime, fine sand, kaolin, organic ash, clays, diatomaceous earths and precipitated silicates. When mixed with stored grain they cause dehydration of arthropod pests by adsorption of cuticular lipids and by abrasion. In the field they are variously formulated into hydrophilic and hydrophobic types. Sprayable formulations of kaolin can disrupt mating, plant recognition, feeding and oviposition of various homopteroids, weevils, moths and mites. Biting pests eating them may die of a blocked hindgut, as in *Cydia pomonella*, *Diaprepes* citrus weevils and *Tetranychus* mites (Showler, 2002). Dusts rarely affect plant growth adversely, but are easily washed off by rain. Calcium silicate applied to the soil in South African cane fields (Kvedaras *et al*., 2007), reduced the growth rate and survival of pest *Eldana saccharina* (Section **4.4.3(a)**).

13.2.3.5(g) MISCELLANEOUS PHYSICAL METHODS. Soil compaction is associated with tillage (Section **13.2.3.5(a)**), but impaction has long been used to kill insects in flour mills. Recently, ultrasound has been employed on experimental *Drosophila* to disrupt development. Sampling insects with vacuuming devices has had long use (Johnson *et al*., 1957; Southwood, 1978) and employed to reduce populations of *Lygus lineolaris* on strawberries (Rancourt *et al.*, 2000). Air speed at the nozzle must be ~100 km/h. Where labour is cheap such devices might be used more widely to remove pests (especially Hemiptera) from field and orchard crops. Where electricity is unavailable, modified engines from model aeroplanes could power them. Applying BABA, β-aminobutyric acid (Section **2.4.2**), is something of a hybrid method. When various concentrations of it (25–500 mM) are applied to plants it induces them to marshal their own defences against enemies such as pathogenic organisms, nematodes and insects (Tiwari *et al.*, 2013).

13.2.4 Environmental methods: Biological

13.2.4.1 General introduction

Diverse techniques are available. Traditionally, ecologically based methods employ enemies of the focal species: predators, parasitoids, parasites and pathogenic micro-organisms. But increasingly methods using genetic engineering (GE) are being developed, which either involve the pest itself or its resource base. In the former, the pest is genetically modified by introducing selfish elements (Hastings, 1994). In the latter, crop plants, namely part of the external environment, are genetically modified to resist insect attack. Two great advantages of biological methods are that they do not result in chemical poisoning of the landscape, and that some are *intrusive,* namely they spread in a pest's population far from the point of introduction.

We saw in Section **12.3.4.4** that the gross supply and spatial distribution of resources, a bottom-up effect, may determine the mean numbers of many insects at the habitat or landscape level: increase the number of suitable patches and the overall population level increases. Recall too the example in Section **9.3** of the density of cabbages (patches) in a hectare plot (habitat) on the numbers of *Brevicoryne* living there: more cabbages more aphids. While in most crops we aim to increase the biomass density of the product, this increases the resource base of pests attacking it and potentially their mean population density in the field. But there are many cases where insectan enemies kill a high proportion of their pest victims (Cornell and Hawkins, 1995). Indeed, the success of many biocontrol programmes is evidence that they can and do suppress the numbers of pests. So we consider here these two influences, *bottom-up and top-down processes in relation to pest control* (Sections **10.1** and **11.1.1**). This rationale, relating economic control to population dynamics (Walter, 2003), classifies the various biological methods of pest control in agriculture, medicine and animal husbandry. But recall (Andrewartha and Birch, 1984; Polis and Strong, 1996; Jones *et al.*, 1997) that trophic links and other influences are complex. Firstly, we examine resistant crop varieties, which are effectively manipulations of the pest's resource base.

13.2.4.2 Bottom-up: Resistant crop varieties, including those produced by genetic engineering

Plant resistance comprises the collective heritable characteristics by which a plant species, race, clone or individual reduces its successful use by an arthropod species, biotype or individual (Dent, 2000). Even so, weather also affects plant resistance, as in wheat and rice, and herbicides may temporally reduce it (Wu *et al.*, 2004). Dent's definition includes individual variability in natural populations, so producing a *heterogeneous* resource base for herbivores. They have *variable*, often *considerable* physical and chemical resistance to insect attack (Section **2.4.2**). By contrast, *uniformity of product* is required for processing and marketing, which run counter to natural systems and the goal of having a pest free crop. Indeed, crop breeding has traditionally produced cultivars that *require* the use of pesticides (Bottrell and Adkisson, 1977). Resistant varieties are thus *relative* to their susceptible cousins (Bergelson and Purrington, 1996). Then, despite arguments about yield drag (Section **5.3.1.2(d)**), in which resistant varieties are less productive, an analysis by Foyer *et al.* (2007) questions the concept's validity. Trade-offs are not universal. In this connection, also consider *ecological efficiency*.

During the Industrial Revolution, when selective breeding for better crops was progressing, genetics was unknown, although the French polymath Pierre de Maupertuis (Section **11.1.2**) had inklings about particulate inheritance and evolution circa 1750. But not until 100 years later did Naudin, a French botanist contemporary with Mendel, like the Abbé, argue for this form of inheritance. Varietal resistance was not understood and during breeding for greater production and palatability some of this natural defence against herbivores was reduced by default. Today, plant breeders produce many insect-resistant crop varieties. Germplasm banks, usually seed collections, are held by agricultural research stations worldwide, serving as sources of variation for breeding new cultivars. These often combine productivity *and* enhanced resistance. Many test varieties can be produced rapidly if the anthers are removed from flowers, so assuring out-crossing (Section **8.2.1.1**). Wild relatives of crops are a further, natural source of genetic variation, but new heritable variation can be produced artificially by chemicals such as colchicine, by irradiation, or more recently by GE. Furthermore, 'resistance' has two aspects: reduction of pest numbers and tolerance of being eaten.

Long-lasting resistance to insects by crops, while desirable, is constrained by natural selection, although its undoing is likely to be slower when several genes code for it. Pest individuals less affected by the form of resistance have greater RS and so their genes conferring this defensive ability spread. A related factor, as we noted, is the level of genetic variation in a crop. In small-grained cereals (wheat, rice) plants are rather uniform, variation being due to environment. While out-breeding crops like many top fruits are inherently variable genetically, orchards are usually planted with uniform stock. So pollination results in uniform fruit. This homogeneity desired by retailers, naturally influences the success that pests have in destroying a crop, a success that could increase with closer adaptation. If production were doubled in a new cultivar, but losses due to pests increased from say, 10% to 20%, we would still get a big increase (78%) in yield, an effect occurring in new rice cultivars. But maintenance or enhancement of innate resistance to pests is an ideal, one unlikely to have environmental backlash. Nor is extra labour needed.

Biotechnology allows the rapid development of new cultivars, especially in cases in which the appropriate genes are lacking (Bradshaw, 1991). It allows genes from, say, a wild relative to be transferred directly into a potential cultivar, although we recall that the *genetic background* in which the gene is located also has effects (Bergelson and Purrington, 1996), a principle Fisher suggested long ago. By sourcing useful genes from a wider sphere, GE has allowed, for example, the gene expressing toxins from *Bacillus thuringiensis* to be inserted into the genome of many crops, which thus become resistant to caterpillars (Section **13.2.4.2**). Such genetically modified organisms (GMOs) are now planted extensively (Sisterson *et al.*, 2007). Transferring genes coding for the toxin lectin from snowdrops, *Galanthus nivalis* (Amaryllidaceae, Fig. 13.6), dubbed GNA, is being researched for use in apples, tomatoes, potatoes, rice and sugar cane. This toxin interferes with nutrient uptake across the pest's midgut epithelium (Fitches *et al.*, 1997, in Tomov *et al.*, 2003), but might have unwanted effects on parasitoids (below), and ourselves. GE allows us to produce insecticidal proteins and peptides and deliver them to pests via bacterial, baculoviral or plant systems (Casida and Quistad, 1998). Unlike insecticides they stay throughout the plant's life. Such technology is just beginning. We might transfer genes conferring resistance to insecticides in pests into their enemies; even construct genomes in cereals that allow them, like legumes, to fix atmospheric nitrogen. A basic problem with GMOs is predicting what will happen when they are released (Williamson, 1991, 1992). But while subtle problems may arise from their use (below) these should be far less than those resulting from routinely applying insecticides (van Emden, 1999).

When chemical resistance is improved it must not compromise the plant's palatability to us, as with the enhanced levels of protective mustard oils in brassicas. Here, two volatiles, tetradecene and dodecene, sourced from resistant soya beans, repel the moth *Trichoplusia ni* (Renwick and Chew, 1994; Section **5.2.1.4(m)**). Physical resistance of an edible crop plant can often be augmented without reducing palatability, especially if the marketable parts are not the site of resistance. Thus, maize cultivars with tough nodal septa prevent boring by

Fig. 13.6. Snowdrops, the source of the toxin lectin, which can be transferred to other plants by genetic engineering. Source: Wikimedia Commons, author Tim Green.

Diatraea larvae (Section **4.4.1.1(c)**) and potato varieties with glandular hairs on their leaves entrap aphids. In some carrot cultivars, like Regulus Imperial, the foliage does not attract ovipositing *Psila* (Guerin and Stadler, 1984). In rice, high densities of silica grains in surface tissues blunt the tiny mandibles of larval *Chilo suppressalis* (Section **4.4.1.1(c)**) attempting to invade (van Emden and Service, 2004). Similar resistance occurs to another pyralid borer, Scirpophaga incertulas (Bandong and Litsinger, 2005). To digress, in terms of macroevolutionary changes, the drying climate of the Miocene led to the spread of extensive grasslands, the precursors of our grain crops. Erstwhile forest herbivores such as primitive horses began to feed on them, but the grasses evolved siliceous inclusions in their tissues that wore down the horses' teeth. In turn, horses evolved continuously growing (hypsodont) teeth. This is the possible path for grain crops having silica in the first place and many grasses now have opaline phytoliths of silica in their surface layers providing a defence against mandibulate herbivorous insects (Massey *et al.*, 2006). Such defences may cause deterrence, increased mandibular wear, slower growth of the pest and in train a Williams' effect.

Resistant plant varieties often retain their effectiveness against pest insects, although not against plant pathogens. A reason may be that pathogens normally have much shorter life cycles, thus permitting rapid evolutionary adaptation (Hamilton, 1980). Further, if the resistance mechanisms were based on multiple genes they might well pose enhanced difficulty for the pest, a situation relating to the longstanding 'gene-for-gene' hypothesis (Flor, 1942; van der Plank, 1963; Kaloshian, 2004). Here it is supposed that a single gene for resistance in a plant is matched by one nullifying it in the pest or pathogen. Such gene-for-gene resistance was thought to obtain for *Nilaparvata lugens* (Section **5.3.1.2(d)**) on resistant rice cultivars, but later work indicates a polygenic mechanism (Denno and Roderick, 1990). Indeed, lasting resistance is generally polygenic.

We noted (Section **2.4.1**) that plants avoid attack in space and time, the agricultural equivalent being crop rotation. Special early or late sown varieties avoid the brunt of attack by a specific pest, or can be harvested and destroyed with the brutes in the crop, exemplifying the temporal effect. In cotton, it may be adequate to leave a gap of a few months between plantings, although one of its major pests, the pink bollworm, is a long-distance migrant arriving at any time if the weather is warm enough. Then, using several crop cultivars may reduce the impact of fungal pathogens, as it is does in small-grained cereals (Matson *et al.*, 1997).

Finally, GM varieties *may or may not* have complex effects on both the pest and its enemies (van Emden, 1966, 1999; Lövei and Arpaia, 2005). These plants could have primary effects on the pest, but also secondary ones on its enemies, reducing their RS (Section **11.5.2.3**), whether the latter are natural or employed in biocontrol. There are many cases where no ill effects on predators ensue. For example, Cry3A potatoes on *Coleomegilla*, a ladybird predator of Colorado beetles (Riddick and Barbosa, 1998; Section **5.2.1.2(c)**), GNA apples on the ladybird *Adalia bipunctata* (Down *et al.*, 2000, in Sétamou *et al.*, 2002), *Bt* maize on the bug *Orius insidiosus* (Al Deeb *et al.*, 2001; Section **8.2.2.3(c)**), *Bt* maize pollen on the spider *Araneus diadematus* (Ludy and Lang, 2006) and *Bt* cotton on *O. tricolor* and the lacewing *Chrysoperla carnea* (Sisterson *et al.*, 2007).

However, in laboratory studies there were negative effects of GNA-modified crops on three parasitic wasps that feed on aphid honeydew (Romeis *et al.*, 2003). In GNA sugar cane, the borer *Eoreuma lofini* is parasitized less often by *Parallorhogas pyralophagus* (Braconidae) (Tomov *et al.*, 2003). But no such effects occur on parasitism on the cane borer *Diatraea* by *Cotesia flavipes* (Sétamou *et al.*, 2002), which could relate to different modes of searching by the wasps. In the laboratory, using *Heliothis virescens* on tobacco expressing low levels of *Bt* toxins, there were differences on two parasitoids, *Campoletis sonorensis* (Ichneumonidae) and *Cardiochiles nigriceps* (Braconidae) (Johnson, 1997). Host larvae grew slowly on *Bt* tobacco, giving a Williams' effect in which *Campoletis* parasitizes more of them. A synergistic effect between toxin and parasitoid on the pest's larval survival also occurred, a link absent in *Cardiochiles*. *Coccinella septempunctata* ate more *Aphis fabae* on resistant 79S4 faba beans than on normal cultivars (Shannag and Obeidat, 2008). Johnson notes that physical factors have overall control in the field, leading to the perennial point that laboratory results may be inapplicable to the field (Lövei and Arpaia, 2005; Sisterson *et al.*, 2007; Clark *et al.*, 2012; but see Poelman *et al.*, 2009). Thus, due to density dependence, low density of a pest due to GM could result in less mortality from enemies, different from the

Aphis–Coccinella case above. Endoparasitoids, having a more intimate association with their hosts than predators have, may well suffer more. But the bottom line is crop protection, not saving enemy insects. Despite resistant cultivars sometimes reducing the RS of enemies, the combined effect may give better control. Such complexities must be evaluated against the background of reduced use of those insecticides that may kill a pest's enemies to the extent of entire local destruction.

13.2.4.3 Bottom-up: Resistance in man and livestock

For human populations and livestock, repeated exposure to diseases, whether insect-borne or not, gradually increases natural resistance over time by the universal process of natural selection. The results of successive epidemics of plague in 1720 and 1722 in Marseilles, France, when far fewer deaths occurred in the second wave (Section **7.2.2.2**(**b**)), is a probable example. This is augmented by acquired immunity. Clearly, these processes are comparable to the development of bottom-up resistance in plants. The resistance of Europeans to many diseases originating in their domesticated animals assisted their conquest of the Americas, diseases to which indigenous peoples were susceptible (Diamond, 1999). Today, many Indians in the Subcontinent resist vivax malaria (Herrel and Amerasinghe, 2004). Natural selection in malarious areas has also driven the spread of the sickle cell gene (Section **7.3.2.4**(**d**)). In Africa, resistance by some native cattle breeds, such as the Muturu (Fig. 13.7), to the trypanosome causing nagana (Section **7.3.2.4**(**m**)) has also evolved.

13.2.4.4 Bottom-up: Alternative food, trap crops and intercropping

Spruce trap logs have been used in Europe to catch *Ips typographus* for over 200 years, while Curtis (1860) suggested using trap crops in agriculture. But they have been employed sparingly. In essence, they depend on a pest preferring certain species, cultivars or stages of growth (Hokkanen, 1991). Also, plants other than the main crop increase diversity. The resulting polycultures often reduce pest damage (Risch, 1981) when monocultures would not, an effect employed in intercropping. Thompson (1939) asserts that the sub-division of habitats is 'undoubtedly the primary extrinsic factor of natural control'. For agriculture, trap crops can catch and manipulate pests at the crop edge, within-crop, within-farm or on landscape scales (Hokkanen, 1991; Shelton and Badenes-Perez,

Fig. 13.7. N'Dama cattle in West Africa. A breed resistant to bovine trypanomyasis. Source: Wikimedia Commons/ILRI.

2006). For the landscape, co-operation among local farmers is essential. Trapping reduces the need for chemical pesticides, being a rational and profitable component of IPM. Logical parallels to trap cropping exist when domesticated mammals divert biting flies from people. So, trap crops may attract, divert, intercept and retain potential pests. They may be deployed as barriers between the crop and the expected direction of immigration, called *perimeter trap cropping* (Boucher *et al*., 2003), or interspersed in the crop itself, where they are often effective (van Emden, personal communication; Section **13.3.2.3**). In Connecticut, USA, Boucher *et al*., (2003) found that a perimeter of hot peppers reduced damage to bell peppers by *Zonosemata electa* (Tephritidae) from ~15% to ~2%. For some *Anastrepha,* their daily flights from the crop to resting places outside it (Aluja, 1996) facilitates trapping. Traps may also interfere with the pest's ability to damage plants. For tomatoes, using potatoes to trap Colorado beetles (Section **5.2.1.2(c)**) can increase yield by >70%. Tall plants provide a physical barrier, but work best if they constitute a preferentially attractive resource in which, none the less, potential pests have poor RS. Pests may then be destroyed, for example, with an insecticide, but of course this has the potential disadvantage, apart from cost, of also destroying the pest's enemies (below).

Trap crops deployed early in the season can intercept migrant pests that try to breed in them but do not survive in them, so functioning as population sinks. Yellow rocket works like this for diamondback moths. In South Africa, Napier grass (*Pennisetum purpureum*) varieties strongly attract ovipositing females of *Chilo partellus* (van den Berg, 2006), an important pest of maize (Section **4.4.1.1(c)**). But while larval survival is poor on this trap, some young larvae leave it by ballooning. Early potatoes expressing *Bt* toxin, planted along field edges, trap immigrant Colorado beetles, the main crop being planted later. In all cases the area ratio of the trap to the main crop must be adequate, normally 2–10%. These traps may be sprayed with semiochemicals attractive to the pest, but this is usually temporary and expensive. In trap cropping for *Anthonomus grandis*, marginal plots can be treated with the synthetic pheromone 'grand lure' to improve their efficiency (Hokkanen, 1991). But if such traps were genetically engineered to produce attractants themselves it would be better (Nesnerova *et al*., 2004, in Shelton and Badenes-Perez, 2006), a very 'green' method indeed. Recall (Section **4.2.1.2(h)**) that some plants naturally produce insect JH mimics. Finally, some trap crops, such as *Bt* collards (*Brassica oleracea* var. *acephala*), may be an additional marketable product, as is Napier grass for fodder and fever grass (*Cymbopogon flexuosus*) for a variety of products. While trap crops are normally planted before the main crop, thus catching early pests, they can be deployed later to reduce local pest density. Thus, for pests such as several beetles and some heteropterans that overwinter in naturally insulated micro-environments, a mulch trap can lure them into false security, as this blanket can be removed when low temperatures preclude their further movement (Milner *et al*., 1992).

While growing main and ancillary crops together is primarily a bottom-up technique affecting the resource base, it can have secondary, top-down results by providing micro-environments where a pest's enemies thrive. In Canada, brome grass *Bromus sterilis*, used as a 15 m border around wheat, attracts *Cephus cinctus* (Section **4.4.1.1(b)**). Later on, parasitoids emerge that spread into the crop. In Kenya, maize intercropped with molasses grass *Melinis minutiflora*, suffered only 4.7% loss from stem borers, while control maize plots had 39.2% loss (Khan *et al*., 1997). This grass produces several volatiles that repel the borers *Busseola* and *Chilo*, but strangely attract parasitoids, such as *Cotesia sesamiae*. Also, in West Africa, maize is used to trap the cane borer *Eldana saccharina* (Section **4.4.3(a)**). When the egg parasitoids *Trichogrammatoidea* and *Telenomus* were released there, they reproduced faster in the trap crop than in the cane, so enhancing top-down control. Some cruciferous weeds attract *Plutella xylostella,* but its ichneumon enemy *Diadegma* becomes abundant in this case (Idris and Grafius, 1996). Even so, *D. semiclausum* finds *P. xylostella* less easily in mixed brassicas (Gols *et al*., 2005), suggesting that such an effect would promote greater stability in a host/parasitoid interaction.

Pleasing techniques like these grade naturally into the all-embracing one of CBC (Section **13.2.4.7**). Even so, insects formerly on weeds, such as *Dectes texanus*, a cerambycid borer of *Xanthium* spp., have spread to crops. And in West Africa, attacks from cassava mealy bugs (Section **3.3.3.1(b)**) are more severe in polycultures (Ngeve, 2003). We need more specific research. A further development is the so-called *push-pull strategy* (Cook *et al*., 2007). Pests are diverted from the protected resource (push) while being attracted to a diversionary one (pull), wherein they may be destroyed. The dual effect should be more efficient than either component used alone.

Trap crops may be compared to keeping domesticated animals as bait to reduce vectors of human disease (above), as in many traditional agrarian societies. But it may be hard to discover if they act as a trap, a diversion, or serve to extend the vector's food base. Keeping such animals close by may induce mosquitoes and black flies to bite them, not us. But as usual there are complications. First, there are anthropophilic and zoophilic biters (Sections **7.3.2.4(d)** and **7.3.2.4(e)**). Indeed, future studies on the neuromuscular and genetic bases of host preference in anophelines may allow us to modify this trait to effect malarial control (White *et al*., 2011). Second, livestock provides alternative food, increasing the local carrying capacity for such flies, so enhancing their populations. This recalls the case of cassava mealy bugs in polycultures (above). In the present case, when alternative, diversionary food is provided efforts must be made to eliminate breeding sites especially where cattle are watered. Indeed, some mosquitoes breed in water-filled hoof prints (**Fig. 13.8**). In India, the Plague Commission used diversionary guinea pigs as they are much favoured by fleas (Section **7.2.2.2**). In one case ~1000 of these irritating beasts were found on a single, unfortunate living trap (Rothschild and Clay, 1952).

13.2.4.5 Top-down: Microbial agents

Microbial agents comprise mainly pathogenic fungi, protozoa, bacteria and viruses, although Fuxa (1987) and others include nematodes in this group. Fungi infect on contact, but to gain access to their hosts the other groups rely on being eaten or being transmitted by a vector. Most of them are destroyed or inactivated by UV light on foliage, by aridity and by adverse temperatures. Even pH, particularly acid foliar exudates, can give protection. These agents also have their enemies (Rosenheim, 1998), which include Collembola, beetles, mites, nematodes, fungi, bacteria and viruses. Pathogenic transmission can be *vertical* or *horizontal*, namely via a host's ovum or by infection from a conspecific host or other organism (Section **7.3.2.4**). Vertical transmission can maintain pathogens in sparse host populations (Fuxa, 1987). For control most of the microbial market comprises *Bacillus thuringiensis* in its various forms (below). But other types are coming in, the market expanding by >10% annually, and better ways are being sought to integrate their use with chemical pesticides.

Fig. 13.8. Buffalo wallowing in mud in South Africa. Several anopheline mosquitoes breed in such small water bodies. Source: Flickr, amanderson2.

If these organisms are used as live preparations they are true biological agents. If compounds derived from them are used they are not (Section **13.2.3.2**). Living, reproducing agents are capable of undergoing co-evolutionary change (Section **8.2.1**) with the pest, such application being called *inoculative augmentation*. When dead, the term is *inundative* or, better, '*insecticidal' augmentation*. Although living preparations are less likely to suffer from acquired resistance by the pest, most applications have been the latter. A frequent disadvantage is that live preparations can take several days to kill the pest, crop damage meanwhile continuing. Similarly, in classical biological control there is a preference for using agents that act early in the pest's life cycle (Godfray, 1994).

While pathogenic fungi can normally be employed only in humid environments, they are potentially the most versatile group. They are often virulent, if rather slow acting, and attack several stages of a broad range of pests. Spraying them with water promotes sporulation. *Beauveria* spp. are used against caterpillars, including larval *Ostrinia*, *Leptinotarsa*, *Cylas* spp. and *Hypothenemus*. They show promise against western flower thrips in glasshouses. *Verticillium lecanii* and *Paecilomyces fumosoroseus* have been used on aphids and whiteflies there, one in which humidity can be regulated, while *P. fumosoroseus and P. farinosus* worked well in trials with *Delia antiqua* (Poprawski *et al*., 1996), killing pupae and rendering adults infertile. *Metarhizium anisopliae* is often effective against pests in the soil, like termites and scarabaeid grubs such as *Melolontha* and *Oryctes*. This fungus causes green muscardine disease of locusts (**Fig. 13.9**) and ULV (ultra-low volume) spraying the spores with oil protects them from desiccation in arid environments and minimizes water use (Bateman and Alves, 2000). Research continues to develop suitable strains and improve formulations that will reduce locust populations to densities where they do not swarm. Presently, *M. anisopliae* var. *acridum* strains are used, IMI 330189 in Africa, F 1984 in Australia and CG 423 in Brazil. While the short shelf life of the conidia has been a problem, largely because they are hygroscopic, new techniques allow storage for up to 4 years (Lomer *et al*., 2001). The best field results, >6 weeks infectivity, are for IMI 330189 in Niger.

The fungus *Entomophthora maimaiga* suppresses gypsy moths (Weseloh and Andreadis, 2002), while the decline in Nova Scotia, Canada, of another tussock moth, *Orgyia leucostigma*, which had virtually disappeared by 2001, is associated with the presence of *E. aulicae*. In fields, *E. muscae* has been effective against *Delia antiqua* (above), while *Zoophthora phytonomi* attacks the larvae of the weevil *Hyperia postica* (Harcourt, 1990). Trials financed by the World Health Organization with such genera as *Culicinomyces* and *Coelomomyces* are yet to be extended as effective methods of control for dipteran vectors of disease. *Lagenidium giganteum* is an aquatic fungus that attacks larval mosquitoes. These fungi present little risk against non-target organisms and are usually simple to produce, but they have a short shelf life if not refrigerated and may be destroyed by sunlight. Many mosquito species, however, prefer shaded places for breeding (Section **7.3.2.4(d)**).

Fig. 13.9. Green muscardine disease of locusts caused by the fungus *Metarhizium anisopliae*. Source: Wikimedia Commons, CSIRO.

Within the Protista, the Neogregarina may turn out to be useful, especially against aquatic and soil-dwelling Diptera. The Microsporidia, a phylum unrelated to other acellular organisms, contains *Nosema locustae*. Its use against grasshoppers on rangeland provides a rare case of effective control by this group. But *N. pyraustae* has been successful against *Ostrinia nubilalis*, and its delivery improved when Lewis and Lynch developed a method of lyophilizing, vacuum drying and storing this pathogen (Brindley *et al*., 1975).

Many bacteria can be cultured in appropriate media, producing vast numbers. They are less affected by desiccation than fungi, and their usual impact lies in toxin production. Bacterial preparations are normally powders containing ~1000 parasporal bodies/mg. But only a few bacilli are used commonly. These are mainly varieties of *Bacillus thuringiensis* (*Bt*), especially var. *israelensis,* discovered in the Negev Desert in 1976 (van Emden and Service, 2004). *Bt. israelensis* and *Bt. alesti* can be used against *Ostrinia* and are effective under certain physical conditions. But they lose pathogenicity in a few days of strong sunlight and/or temperatures >32°C. Living *B. sphaericus* control some mosquitoes and are often persistent. *Bt. popilliae* kill scarabaeid beetles, especially *Popillia japonica* (Section **3.2.1.2(b)**) and other pest insects in the soil. But because these bacilli afflict a broad range of pests their potential to destroy native insects must be considered. A *Brevibacillus laterosporus* strain, isolated from soil in Sardinia, is toxic to *Musca domestica*, mosquitoes and black flies (Ruiu *et al*., 2005). Since it affects honey bees and is lethal to several other insects, however, its use is limited. Species of *Serratia*, including *S. piscatorum*, *S. entomophila* and *S. marcescens* attack insects, but specialized viruses called *bacteriophages*, which are widespread, can destroy entomopathogenic bacteria. On a rather different tack, freeze-dried preparations of the bacterium *Pseudomonas syringae* promote ice nucleation in overwintering Colorado beetles, reducing their cold hardiness (Lee *et al*., 1994). Similarly, *P. syringae* and especially *P. putida*, both living and dead, reduce cold hardiness of pear psyllid bugs (Lee *et al*., 1999; Section **10.2.3.3**). Note that here, quite atypically, a biotic factor influences the severity of a physical one.

Endopathogenic nematodes, such as *Steinernema* and *Heterorhabditis*, while not true micro-organisms themselves, have a Gram-negative symbiont, the anaerobic bacterium *Xenorhabdus*. So, these nematodes are effectively motile packages of bacteria. Infective third stage juveniles enter the insect's body via the mouth, anus or spiracles and release their deadly symbionts, usually killing the host with toxins within 48 hours (Kaya and Gaugler, 1993; Bowen *et al*., 1998). These nematodes are effective in the soil and have been used against scarabaeid larvae (Villani and Wright, 1988), root weevils (Jaworska and Wiech, 1988) and *Anastrepha* larvae (Toledo *et al*., 2006). *Metaparasitylenchus hypothenemi* reduces AF in *H. hampei* (Section **6.3.1.1(b)**). But they desiccate easily (Georgis *et al*., 2006) and bacteriophages limit the effectiveness of their symbionts. They are also used in foliar sprays (Arthurs *et al*., 2004), where agents to reduce desiccation and improve 'sticking' should be employed. In glasshouse trials, *S. feltiae* gave >90% mortality of *Bemisia tabaci* on a variety of crop plants (Cuthbertson *et al*., 2007). Again, surface moisture is essential to achieve control.

Nematodes also have their enemies and are eaten by Collembola, mites, tardigrades, other nematodes, and ensnared by specialized fungi. However, experimental work is currently underway to assess their use against strawberry crown moths (Section **4.2.1.2(l)**) and some other sesiid borers. Several nematodes occur naturally as enemies of bark beetles, such as *Sulphurethylenchus* (Ashraf and Berryman, 1970) and *Heterorhabditis* (Garraway and Freeman, 1990), while *Deladenus siricidicola* has been used to control wood-boring *Sirex* larvae (Section **4.2.1.2(j)**). Arthurs *et al*. (2004) give an extensive table of their use.

Although several hundred viral species have been isolated from insects, only a few are produced commercially for IPM. Most useful are the baculoviruses comprising granulosis viruses and nuclear polyhedrosis viruses (NPVs). They evolved as common pathogens of insects, are confined to arthropods and can control *Oryctes* beetles (below) and *Tipula paludosa* larvae. Fears that they could adapt to attack vertebrates are unfounded, many are specific to insectan hosts and anyway, all occur in natural environments. Formerly, they were often used for inoculative augmentation. But with the advent of GE they can be greatly modified, for example, a baculovirus expressing snake venom (van Emden and Service, 2004), hence extending their use. Their potential impact on native arthropods, however, must be appreciated (Williamson, 1991). Thus, they are spread in the wind and on birds' feet. For gypsy moths the impact of NPVs is reduced when larval food is tannin rich, as in red oak (Elkinton and Liebhold, 1990), since this limits their passage through the peritrophic membrane. Baculoviruses may also be constrained by pathogenic bacteria.

13.2.4.6 Top-down: Classical biological control

Early efforts at biocontrol used avian predators. For millennia the Chinese have used ducks to eat pests in rice paddies, with the advantage that the control agent can be converted into a crispy treat when its predatory life is over. Similarly, fishes are used in this situation. Mynah birds have been used also, but are apparently inedible and patently garrulous. It seems possible that an insectivorous bird(s) could be domesticated and bred selectively for biocontrol, and free-range chickens as well as ducks provide existing examples. Starlings and jackdaws are possible candidates: they feed in sizeable flocks on the ground and have a strong *aggregative response* (Sections **10.2.3.9** and **11.5.2.2(b)**). Hartman and Hynes (1977) record starlings eating *Tipula* larvae under cow pats. Flocks of sea gulls in many inland areas and migrant storks in the Great Rift Valley eat insects on newly ploughed fields. Birds naturally suppress insect damage to white oaks (Marquis and Whelan, 1994). However, without an aggregative response involving large numbers, biocontrol with vertebrates is unlikely to work against explosive pest populations, as seen by Howard and Fiske (1911), as they cannot breed fast enough to respond (i.e. the *numerical response*; Section **10.2.3.9**), to match the expanding numbers of their insectan prey.

Indeed, concordant with the verity of top-down control (Price, 1988; Berryman, 1996), entomophagous insects are almost invariably used in biocontrol of pest insects (Debach and Rosen, 1991). Again from ancient times, Chinese citrus growers used the ant *Oecophila smaragdina* to combat leaf-feeding insects (Caltagirone, 1981). An early, unsuccessful case employed the braconid wasp *Cotesia* (= *Apanteles*) *glomerata* against Pieris in Canada. Later, *A. rubecula* proved to give some control (Parker and Pinnell, 1973). An early, successful case was the suppression of *Icerya* populations on Californian citrus by vedalia beetles (**Fig. 13.10**; Section **4.3.5**) imported in 1888 from Australia. Its success was matched only by its cost effectiveness, and led to a spate of research effort, particularly in California (Caltagirone and Doutt, 1989). Caullery (1922, in Thompson, 1929) remarks:

> Les Insèctes entomophages, sont aussi l'agent régulateur naturel de beaucoup le plus éfficace, de la multiplication d'un très grand nombre d'Insèctes, avant tous des Lepidoptérès. En particulier ils constituent un farceur de premier importance dans la lutte contra leur propagation excessive …

an early top-down perspective. By 1935, 26 cases of effective biological control had been recorded (van Emden and Service, 2004), often after an exotic, herbivorous pest had become invasive (Section **8.2.2.1**).

Success of biocontrol has been ~30% (Thacker, 2002), although some estimates are lower (Williamson and Fitter, 1996; Gurr and Wratten, 1999; Louda *et al*., 2003). We hear more of success than of failure. For parasitoids, unless >32% parasitism results, control is unlikely (Hawkins and Cornell, 1994). This is very 'rule of thumb', what is needed for control is a sustained density-dependent response. Biocontrol has had greater success in orchards and forests (mature ecosystems) than in field crops (ephemeral agro-ecosystems) (Varley, 1959; Price *et al*., 1980). The best results have been obtained by using specialized parasitoids (Debach and Rosen, 1991). One attempts to create a pest/natural enemy relationship in the new environment (Daane *et al*., 2015). But of course this depends on several physical and biotic factors. Even so, in over 100 years of biocontrol, pests have been rarely exterminated (van Lenteren *et al*., 2006), continuing efforts being required. Indeed, when detailed post-release studies are lacking, one is unsure of the exact dynamic: if pest densities fall it is tempting to assume the new agent is responsible (Walter, 2003). This is merely association, not proven causation.

Fig. 13.10. The famous vedalia beetle. See also Fig. 8.4. Source: Wikimedia Commons, credit to Katja Schulz.

The rapid increase of exotic pest populations freed from natural enemies, however, supports the idea of top-down restraint (Berryman, 1996), the history of biocontrol in agro-ecosystems providing extensive data on such effects (Section **12.2**). Winter moths in western Canada (Roland, 1994, 1998) and cottony cushion scales in California are illustrative cases. The suppression or extinction of non-target insects (Pimentel *et al*., 1984; Howarth, 1991; Strong, 1997; Lynch *et al*., 2002; Louda *et al*., 2003; Van Lenteren *et al*., 2006; Section

13.2.4.4) is unwelcome evidence of the impact of enemies. But with the advent of DDT, the new insecticides swept away all before as the panacea. As we all know now, this was ephemeral as the effectiveness of chemical pesticides declined and their environmental backlash soon appeared (Carson 1962; Section **13.2.3.1**). For example, many butterflies and moths declined or disappeared from New Jersey after the extensive use of DDT (Simberloff and Stiling, 1996).

At first biocontrol was applied in an *ad hoc* manner. It worked better on pests of longstanding crops in stable agro-ecosystems, like cassava, citrus and sugar cane. In the 1960s the Hairston-Smith-Slobotkin (HSS) model was influential (Hairston *et al*., 1960; Section **10.2.2.5**). Southwood (1977), applying demography, suggested biocontrol should work best on pests near the centre of the *r*- and *K*-selection spectrum (Section **9.1**). But a pragmatic assessment might well be more fruitful (Murdoch *et al*., 1985; Aluja, 1994; Walter, 2003) as biocontrol often fails for lack of autecological knowledge (MacDonald and Loxdale, 2004). Habitat management to suit the introduced agent is often needed (Gurr and Wratten, 1999) as in CBC favouring native enemies. In particular, nectar or honeydew fuel must be on hand for searching parasitoids, as they are necessarily very active. While attempts at biocontrol are wide-scale autecological experiments (Strong *et al*., 1984), they are rather unnatural, not general, as they affect simplified agro-ecosystems. Success is often apparent because of the lack of bottom-up influences. Then again, insecticidal control can be terminated if undesirable, which is not the case when an exotic enemy is released.

Successes in biocontrol have been largely on plant pests. Although they have been used in medical/veterinary situations, results have usually been poor. For plant pests, successes are: (i) in forests (winter moths in Canada by *Agrypon* (Ichneumonidae) and *Cyzenis* (Tachinidae)); (ii) in orchards (the leaf miner *Phyllocnistis* on Queensland citrus by *Ageniaspis*, (Encyrtidae)); (iii) in field crops (the mealy bug *Phenacoccus* on West African cassava by *Apoanagyrus* (Encyrtidae)); and (iv) in greenhouses (whiteflies on tomatoes by *Encarsia formosa*). More examples are given below. One should use insects that attack early in the pest's life cycle as this minimizes crop damage (Section **13.2.4.5**). But for medical/veterinary pests having eruptive, vagile populations (mosquitoes, simuliid and strike flies), success is inherently unlikely. While little fish like *Gambusia* and *Poecilia*, the mermithid nematode *Romanomermis*, the predatory mosquito *Toxorhynchites* and the bug *Notonecta* (Murdoch *et al*., 1985) have been *locally* successful against mosquitoes, they cannot match its patchy, shifting populations. Local success has been achieved in suppressing *Musca domestica* with the wasp *Spalangia cameroni* (Skovgård and Nachman, 2004). These virulent flies are indeed masters of escape in space and time, to an extent employing an *r*-strategy. But even tsetse, with their low reproductive rate and *K*-tendencies, have not been controlled by the wasp *Nesolynx*.

Candidate predators and parasitoids do not just appear, they must be sought. Such an adventure requires special field kills and thorough entomological knowledge. So, the successful practice of biological control involves the following:

1. A search for suitable natural enemies, often in the pest's place of origin, especially in physically favourable areas in which, nevertheless, it exists at low density. Namely, areas in which potential agents may well be suppressing a pest naturally.
2. Thorough taxonomic and breeding studies to ensure the release of a *single* biological species (Walter, 2003). Rearing methods must aim to conserve genetic variation (Bigler, 1989): neither artificial conditions nor economic constraints should impair the agent's quality.
3. A quarantine when any hyperparasites (Section **8.2.2.5**) and any other deleterious organisms are eliminated.
4. Biotypes from different regions should be employed (Caltagirone, 1981; Wang, Q. *et al*., 2008), and climate matching undertaken.
5. Behavioural studies to find out if the introduced agents will indeed contact the host in the new environment. In particular, they should not be released while still showing any migratory urge of the oogenesis-flight syndrome (Johnson, 1969; Vet and Dicke, 1992; Section **10.2.4.1**). It may be necessary to modify the host's new environment to suit the lifestyle of an exotic enemy (Gurr and Wratten, 1999).

Four phases exist in the introduction of any alien species: arrival, establishment, dispersal and range expansion (Memmott *et al*., 2005; Liebhold and Tobin, 2008). For *Arytainilla spartiophila* (Psyllidae), a pest introduced into Otago, New Zealand, the number of individuals (propagule size) was the major determinant in establishment. Survival for the first year gave a 96% chance of persistence. Sometimes even a few individuals were successful. But in general the size of propagules and the number of releases strongly influence the chance of establishment (Williamson, 1996; Williamson and Fitter, 1996; Memmott *et al*., 2005). Then, introductions against specialist as opposed to generalist herbivores, especially those that are exposed, have had greater success (Gross, 1991). Thus, the results of controlling scale insects, which are exposed and sedentary, have been excellent.

When the chosen agent is, hopefully, finally established in the target area, those that enter into a *new association* with the focal pest have a higher rate of success than those showing a previous evolutionary history of interaction with it (Hokkanen and Pimentel, 1989). They explain that a degree of tolerance will not have yet co-evolved and thus suppression of the pest will be greater and more likely. But this is not always so (van Emden, personal communication). In all cases an assessment of potential backlash on species related to the pest in the native fauna is desirable (below). We consider now a few case histories illustrating some relevant principles.

In 1973, *Phenacoccus manihoti* (Pseudococcidae; Section **4.3.7**) arrived from South America onto West African cassava. By 1986 it had spread to 27 countries moving at a rate of some 300 km/yr. *Apoanagyrus lopezi* (Encyrtidae) from Paraguay was cultured and released in Nigeria in 1981. Further releases followed, plus those of two other encyrtid wasps, *A. diversicornis* and *Gyranusoidea tebygi*. But *A. diversicornis* has not done well in Africa, possibly due to interspecific competition with its congener (Pijls and van Alphen, 1996). Neither have two predatory coccinellid beetles, *Diomus hennesseyi* and *Hyperaspis notata*, had much impact. By 1985, however, *A. lopezi* was established in West and Central Africa in an area >600,000 km^2. The several hyperparasitoids present (e.g. *Chartocerus* and *Prochiloneurus* spp.) have not restrained it (Sullivan and Völkl, 1999). One reason for this wasp's success is its effective dispersal and location of its hosts, even when they are at low density. At the patch level it detects them by responding to odours released by freshly damaged plants. Locally, it is highly dispersive (Greathead, 1986). Then, on a wide spatial scale, although many releases were made, its distribution would have remained patchy had it only local dispersal. Work on *Melittobia* shows how effective redistribution may be in another minute parasitoid (Freeman and Ittyeipe, 1976, 1982, 1993; Section **10.2.4.1**). Here, as in its coccoid host, searching is accomplished by huge numbers, not high ISC, just as it is in cestode eggs or wind-dispersed pollen. In 2010, *A. lopezi* was released against pseudococcid bugs on cassava in Thailand.

Populations of *Nezara viridula* (Section **6.3.2.1(a)**) have been managed by biocontrol in many parts of Australasia and the Pacific Islands. In 1933, Australian workers first imported the scelionid egg parasite *Trissolcus basalis* from Egypt (Caltagirone, 1981) and this continued until 1943. While reductions to this pest's populations were achieved, further imports from 1953 to 1963 from Pakistan (successfully) and other places (unsuccessfully) were made, finally achieving effective control. In New Zealand, *Nezara* had become a problem by 1944. In 1949, *T. basalis* was shipped from Australia and the pest declined. Finally, *Nezara* reached Hawaii in 1961 and the next year Australian parasitoids, including the *T. basalis* group and the encyrtid wasp *Xenoencyrtus niger*, were released. The tachinid flies *Trichopoda pennipes* and *T. pilipes* from the Caribbean were added, and a decline to below the EIL occurred. However, work by M.T. Johnson (Louda *et al*., 2003) shows that the most frequent egg parasitoid is *Anastatus* (Eupelmidae) introduced accidentally! Further mortality of the eggs by various ants and spiders, also accidental introductions, may destroy up to 80% of the bugs. These results illustrate the importance of using control agents from different sources: some biotypes work and others do not, another facet of commonness and rarity. So, while it is simple to match gross physical environments of target and source areas, diverse biotic effects, which are more difficult to assess, also may be involved.

But biocontrol often does not work. *Ostrinia nubilalis* reached North America in 1917. By 1925 its devastation was so great that many farmers abandoned growing maize. Although 24 species of exotic parasitoids have been tried, only six became established (Brindley *et al*., 1975), none of them successfully (Clausen, 1978). Thus, ~ 3,000,000 *Bracon brevicornis* (Braconinae) were released at a total of 11 states, but not a single specimen ever recovered. *Lydella thompsoni* (= *grisescens*, Tachinidae) is probably the most widespread agent, but it is attracted to few maize cultivars and only then to the borer, limiting its general use. Levels of larval parasitism rarely exceed 20%. The ichneumon *Eriborus terebrans* is more effective, but fails to penetrate fields far from woodland edges: there is enemy-free space (Sections **9.9** and **10.1**) at the habitat level. *Simpeisis viridula* (Eulophidae) was released in Quebec in the 1930s and 1940s but not found again until 1964. Females do not search the lower level of maize stems, as might be suspected from their metallic green colour (Section **10.2.4.2**): there is enemy-free space within each plant since most susceptible larvae remain below this level. Overall, the success of biocontrol against borers and other concealed pests has been poor (Gross, 1991). *Orius insidiosus* (Anthocoridae), a generalist feeder, kills many young larvae early in the year but later on, rather perversely, prefers maize pollen. Nor can it reach big larvae within the stems. In North Dakota, however, coccinellid beetles and green lacewings were found to kill >70% of the young larvae, although Lee's (1988) life table from Alberta, ~500 km to the north-west, shows that predators and parasitoids had but a small effect there. The major factor is bad weather, which, as Thompson and Parker (1928a) found in France, kills the young stages by desiccation, by heavy rainfall or freezes diapausing larvae. While resistant varieties of maize have been developed they cannot be grown profitably in many regions.

By the 1980s the majority view was that in successful biocontrol the agent imposed a rather stable, low density of the focal pest (Murdoch *et al*., 1985). This was achieved when the agent had become well adapted to its physical environment and its victim and had synchronized with both. It should increase in numbers rapidly and possess good searching ability. Also, minimal lag effects in its response to changes in host density were thought necessary. While these features were held to apply to parasitoids, many cases of successful control by predators exist. Murdoch *et al*. review examples in which this view is incorrect, for example in the sawfly *Pristiphora* (Section **5.2.1.3(e)**), in *Icerya* (Section **4.3.5**) and for various mosquitoes by *Gambusia* (Section **7.3.2.4(d)**).

The reasons for such exceptions depend largely on spatial heterogeneity (Section **12.2**), a feature signally absent from most demographic models (Section **11.5**). In reality, pests may become extinct locally but are unaffected elsewhere. Then, biocontrol agents frequently persist because they find other victim species or are playing 'catch up' with their usual host. The latter is a scenario like that of *Opuntia* cacti in Australia and *Cactoblastis* (Sections **2.4.1** and **8.2.3; Fig. 13.11**). While this moth destroys masses of cactus, isolated plants spring up elsewhere, which it finds ultimately, and so on, an effect expected given the usual view of metapopulations (Section **11.2.2.2**). The rule of pragmatic thumb, however, is: 'if it doesn't work in three years it won't work at all'. But a longer period may be necessary, the establishment phase (above). Weather, by chance, may be harsh when it is introduced and/or the candidate agents may need time to adapt to local conditions. This happened when some coccinellid beetles were brought to North America to control various pests (Michaud, 2012). Results based on demographic expectations, namely from equations as in Section **11.5**, have in general not been borne out. Walter (2003) promotes the view, developed here, that studies based on individual behaviour, which is at the root of autecology (Thompson, 1956; Sections **10.1** and **11.2.2.1**), are more realistic and hence more likely to be successful.

Fig. 13.11. *Cactoblastis* larvae busy destroying an *Opuntia* leaf. The moth brought about a great reduction in the numbers of this invasive weed in Australia. Source: courtesy USDA Agricultural Research Service.

Biological control is not without environmental risk. Introduced agents may have a potential to attack a range of non-target organisms (Howarth, 1991; Strong and Pemberton, 2000; van Lenteren *et al.*, 2006). Apart from pest insects, this has occurred in the biocontrol of weeds. Indeed, traits regarded as desirable for biocontrol, particularly high *r* and vagility, are those predisposing an introduced enemy to have inimical effects on native species (Louda *et al.*, 2003). Interaction with a pest is not simply two-way in which the enemy's impact dies away at a low pest density (Simberloff and Stiling, 1996). Trans-specific mortality (Freeman and Jayasingh, 1975a; Freeman, 1977; Bonsall and Hassell, 1997, 1998; Section **10.2.3.9**) may drive it and other victims to extinction. The unique faunas of isolated islands, such as New Zealand, Fiji and Hawaii, are especially at risk. Biocontrol of the coconut moth, *Levuana iridescens* (Zygaenidae), the only representative of a genus endemic to Fiji, was begun in 1925 employing *Bessa* (= *Ptychomyia*) *remota* (Tachinidae) from Malaya. The aim was pest reduction not extermination, but the last specimen of the moth was seen in 1929 and another zygaenid moth, *Heteropan dolens*, went extinct at this time (Robinson, 1975; van Lenteren *et al.*, 2006, their Table 1). Most likely, extinction occurred via the multi-specific pathways of trans-specific mortality. Then, the suppression of *Nezara viridula* on Hawaii (see above) may have caused the observed reduction in populations of some native pentatomid bugs (Henneman and Memmott, 2001). Indeed, 32% of the 115 parasitoids introduced into these islands for biocontrol have been found to afflict species other than the intended one (Strong, 1997). Employing *Gambusia* fishes to control mosquitoes has been associated with the decline of several native freshwater faunas. There are also a few cases in which an introduced parasitoid has become a hyperparasite of an existing biocontrol agent. Thus, when *Quaylea whittieri* was released in California to control black scale, it attacked and lessened the impact of *Metaphycus lounsburyi* (Encyrtidae) introduced earlier (Pimentel *et al.*, 1984).

The introduction of tetrapods, such as the mongoose and the big cane toad, *Rhinella marinus* (Fig. 13.12), have led to the decline of native faunas in Australia and the Caribbean, although in the latter region habitat destruction is an important additional factor. Most introduced predators kill the native fauna, but with *B. marinus* it is the mammals that eat it that die from its poisonous skin. Starving Cambodians, suffering the deprivations of the Pol Pot regime (1975–1979), skinned the brutes and ate them with impunity!

Fig. 13.12. The cane toad, *Rhinella* (formerly *Bufo*) *marinus*, a poisonous piece of work. Its entry into Australia brought about the demise of several indigenous predatory mammals. Source: Wikimedia Commons, author Froggydarb.

Such impacts have engendered a more critical attitude to biocontrol. In the 1990s the proposed importation of the Australian wasp *Scelio parvicornis* to control rangeland grasshoppers in the USA was resisted for fear of decimating native species (Lomer *et al.*, 2001). One of these grasshoppers, *Hesperotettix viridis*, suppresses snakeweed, which is poisonous to cattle. A fungal pathogen, *Entomophaga praxibuli*, had already been released. Lockwood (1993) gives a restrained account of the bureaucratic muddle on which decisions to release exotic parasitoids and pathogens had been based. Van Lenteren *et al.* (2006) provide details of risk assessment. But while biocontrol involves risk, it is often necessary (Thomas and Willis, 1998). See Huffaker (1971), Huffaker and Messenger (1976), Greathead (1986), Strong (1997), Bellows and Fisher (1999), Strong and Pemberton (2000), Louda *et al.* (2003) and Copping (2004) for further information

13.2.4.7 Top-down: Augmentation of natural enemies and CBC

Although Beeson (1941), Pimentel (1961), van Emden (1965) and Way (1966) were early advocates of these methods, their ideas have been taken up only recently. On the one hand, the approach is close to classical biocontrol, after all if introduced vedalia beetles have been controlling *Iceryia* in California for over a century (Section **4.3.5**) they are pretty much naturalized citizens, although not maintained by CBC. Over longer time scales the distributions of species are, in any case, labile (Coope, 1977, 1979). On the other, the approach grades into conservation (Potts, 1990; Gurr and Wratten, 1999; Landis *et al*., 2000). With the loss of plant diversity in many regions (Matson *et al*., 1997; Keith *et al*., 2009), methods that redress such a retrograde outcome are needed urgently. Our approach must link crop production, floral culture and the natural conservation of pest enemies.

Modifications can be made on three spatial scales (Landis *et al*., 2000): crop, farm and landscape, a concept relating to levels of environmental space (Sections **9.5** and **12.2**), to metapopulations (Hanski, 1998b), and to macro-ecology (Lawton, 1999; Gaston and Blackburn, 2000). Comprehensive management like this is less likely to have bad effects on native biotas. It should prove to be the most 'nature friendly' and sustainable of all control systems. It aims to conserve *and* improve agricultural production concurrently, landscape beautification being a bonus. These aims must be planned and executed by those having deep understanding of the environment, which apart from ecologists include farmers, civil engineers and above all the fortunate few owning large tracts of land who, in my experience, are usually well tuned in. Diverse changes can be made to crops and their environs to increase numbers and/or facilitate the attack of native enemies of pests (Pimentel, 1961; Vinson, 1984; Powell, 1986; Sivinski and Aluja, 2003). Field crops always occupy highly disturbed habitats. So creating permanent areas within the agricultural landscape is a sustainable means of enhancing biodiversity, especially that of useful enemies. But accidents and extreme weather happen. We should learn 'to live with, and to manage uncertainty, rather than trying to control nature' (Lawton, 1999).

Physical modifications within crops and their borders often enhance humidity and provide refuges for enemies. Thus, soil ridges at the edge or better *across* a field planted with *Arrenatherum elatius, Dactylis glomerata*, *Holcus lanatus*, and/or various seed mixtures of other tussocky grasses provide winter refuges for many predatory beetles (Section **8.2.2.4**(**b**); Thomas *et al*., 1991; Landis *et al*., 2000; van Emden and Service, 2004). They are called '*beetle banks*', a fitting *double entendre* (**Fig. 13.13**).

Fig. 13.13. A beetle bank. Banks following contours conserve soil and limit chemical run-off.

They should be ~2 m wide and ~0.4 m above the field level. When built along contours they reduce erosion and so prevent loss of nutrients, agrochemicals and silt. They provide insulated, flood-free refuges (van Dijk and den Boer, 1992) that can be organized to fit in with the ploughing pattern. Over 20 carabid species were found in a wheat field at Rothamsted (Jones, 1976) and 26 species in a beetle bank in Hampshire (MacLeod *et al*., 2004). Densities of such predators were higher than those along field margins and adult beetles exceeded 1000/m^2, a very high density for a predator. Such banks become winter refuges for spiders, corridors for some migrating butterflies, and provide nesting sites for desirable birds such as partridges and hunting grounds for owls. But in spring-sown cereal fields in Sweden, Öberg and Ekbom (2006) found little effect from them on either lycosid spiders or beetles, possibly due to rapid immigration. Large carabid beetles can move ~20 m/h and several of these fields were only <100 m wide.

Weedy fields have the effect of increasing humidity, biologically they provide nectar and alternative hosts for parasitoids and insect food for game birds (Potts, 1990). Growing weedy flowers in Swiss vineyards promoted effective biocontrol, probably for several of these reasons. Where tachinid flies (Section **8.2.2.5**(**h**)) are being encouraged, umbelliferous plants, which have accessible open nectaries co-evolved to accommodate such Diptera, should be provided for nectar. Hogweed, *Heracleum spondylium*, which thrives increasingly along cart tracks in temperate Europe (**Fig. 13.14**), is suitable except where carrots are grown, since it provides alternative larval food for pest *Psila* spp. (Section **3.2.2.1**(**h**)). Parasitic wasps also feed on its flowers and those of several other Umbelliferae, including dill. Beetle banks might well allow such parasitoids to penetrate crop fields more effectively and make corridors between habitats. We recall (Section **8.2.1.1**) that many plants provide amino acids in their nectar, and may act as nutrients for ovarian maturation in these wasps. Other flowers may be suitable for specific cases, but the general point is they should be self-sustaining and perennial. Furthermore, the spatial arrangement of these resources must relate to the ISC of the enemies being encouraged and flower at the right time. Space and time again. In encouraging enemies, recall Forrest's maxim (Section **10.2.5.2**), one must arrange for their early arrival in large numbers, as shown in the successful control of rice pests (Settle *et al*., 1996; Section **13.3.2.2**) and cereal aphids (Öberg and Ekbom, 2006).

Insectary hedgerows, which are rather more extensive, have been established and investigated. Marked parasitic wasps and ladybird beetles penetrated some 100 m into adjacent crops. In Michigan maize fields, parasitism of *Ostrinia nubilalis* by *Eriborus terebrans* was found to be greater at the field edge (Section **13.2.4.6**). Apart from food and shelter for beneficial insects, alternative hosts for parasitoids may be needed. We recall (Section **5.2.1.4**(**a**)) that if *Diadegma* wasps are to assist in controlling *Plutella* they must be provided with a winter host, often *Swammerdamia* residing in nearby hawthorns. Similarly, in California,

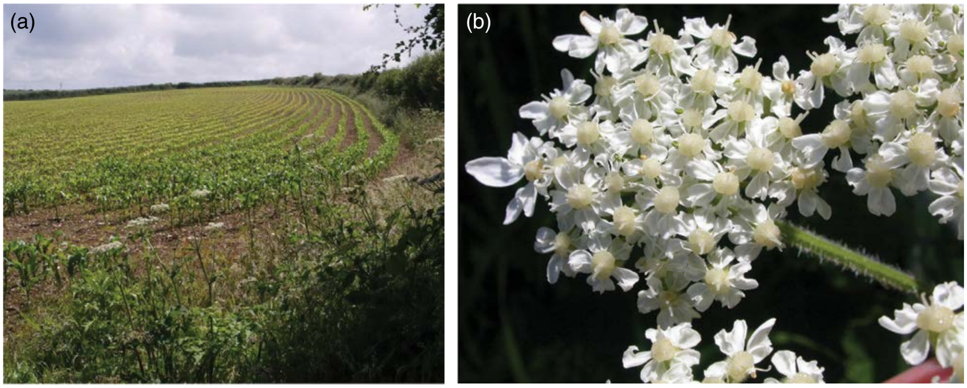

Fig. 13.14. (a) Hogweed, *Heracleum spondylium*, is a common plant in southern England. (b) Such plants with their open nectaries provide copious fuel for many parasitoid wasps in late spring. Source: Wikimedia Commons, credit to Matt Lavin (b) and Derek Harper (a).

Anagrus spp., the mymarid parasitoid of *Erythroneura elegantula*, cannot overwinter in its host's eggs (Section **5.3.1.2(a)**). Other leafhopper eggs occur on *Rubus*, *Prunus* and other trees, which may be grown as crops, or found along streams between the vineyards. But it is possible to encourage the 'wrong' sort of diversity, *Pieris* butterflies, for example, when brassicas are being grown, while some weeds harbour plant viruses.

On a greater spatial scale, windbreaks around fields and orchards protect crops from drying and wind damage but tend to concentrate small migrant insects in their lee (Lewis and Taylor, 1967; Lewis, personal communication). As early as 1949, Flanders (in Andrewartha and Birch, 1954) suggested planting and irrigating oleander around Californian citrus to maintain populations of *Metaphycus* parasitoids against black scale (Section **4.3.8**). Australian citrus may be protected by rows of *Eucalyptus*, *E. torelliana* being especially useful. Rapidly-growing Lombardy poplars with their tall growth form (Section **Fig. 13.15**) make effective windbreaks in temperate regions. But again, note that poplars are the overwintering resource of lettuce root aphids (Section **3.3.3.1(a)**).

CBC includes top-down and bottom-up approaches. At the landscape level a balance must be made between economic and ecological constraints (Letourneau, in Barbosa, 1998). While smaller fields with a higher proportion of hedgerow may promote better biocontrol and use of water, this must be set against the loss of productive area and the increased costs of cultivation. Even so, *the imperatives of agricultural economics must ultimately yield to those of ecology*. Only so much can be done locally. Diversity within habitats, here the crop, is dependent on regional diversity (Lawton, 1999; Section **12.3.4.4(d)**). So it must be promoted on both scales. In Europe, large tracts of land were set aside for hunting and later for ship building timber. Some survive, providing a further source of enemies of pests. In the UK, the practice of growing coniferous soft woods where once hardwood forests existed, should be phased out, as is happening in Germany (Perry, 1998). Such plantations have conspicuously poor biodiversity. Many

Fig. 13.15. Lombardy poplars providing windbreaks in agriculture. Source: Wikimedia Commons, author Maurice Pullin.

suitable areas for siting them exist on barren hillsides in the Pennines, Wales and Scotland, and would beautify the landscape (**Fig. 13.16**). Wetlands provide habitats of great diversity and marshes and carrs urgently need re-instatement, especially those in calcareous areas. In England much time and effort is spent on preserving old buildings: why not more on original habitats? Perhaps because the demands of ecology have given way to those of economics.

CBC is a wide-scale plan for the entire rural environment. *Since so much of our land area is already in crop production*, it dovetails massively into traditional conservation (Margules and Pressey, 2000). The pattern of disturbed landscape can be quantified by assessing the perimeter/area of the component plant communities (Krummel *et al*., 1987). This can then be expressed as a fractal dimension (Mandelbrot, 1977). Furthermore, cereal fields, which comprise 34 million ha in the European Union and 17% of the land area in the UK, must be regarded as part of the total ecosystem (Potts, 1990). To me, the key points are: (i) to stabilize or reduce the rural human population (in many European countries there is zero population growth); (ii) to conserve native biotas while ensuring that control methods cause minimal disruption; (iii) to increase conserved areas especially those woodlands and wetlands rich in species; and (iv) to further increase productivity on marginally reduced crop areas. There is also the principle of how refuge habitats should be connected (Goodwin and Fahrig, 2002). People living in rural districts are usually sympathetic towards conservation and may be induced to assist CBC in various ways. Thus, ornamental ponds and more 'natural' gardens provide fragmented habitats and small havens for many native species. Similarly, the edges of major roads, parking places along them, golf courses and playing fields can be enlivened with a variety of shrubs, trees

Fig. 13.16. A Welsh hillside with firs planted in the foreground, but great areas exist in the distance in which more conifers could be planted.

and other native plants. This is an area in which SADs can be used to assess 'ecosystem health' (Matthews and Whittaker, 2015).

In conclusion, while community ecology allows us to understand the entire rural environment and the species composition of crop habitats, autecology, particularly population dynamics (**Chapters 11** and **12**), concerns the regulation of pest numbers. Diverse agro-ecosystems often provide the greatest potential for stable, moderate numbers of the insect populations in them (Pimentel, 1961; Risch, 1981; Woolhouse and Harmsen, 1987; Barbosa, 1998), populations that are best understood by applying both approaches.

13.3 Integrated Pest Management

13.3.1 General introduction

We now step back from the comprehensive field of CBC to the specifics of IPM in a few contrasted crops. We focus on the confines of the crop, although many biological agents and methods like SMT used in IPM, operate on wider spatial scales. The 'crops' themselves vary in scale from vast coniferous forests to the limits of horticultural plots. The word 'management' is a euphemism, comfortingly implying that we have total control of the agro-ecosystem. Of course, anyone with a slight acquaintance with ecology realizes that our influence is no more than modification (Lawton, 1999), albeit an effect that has often been detrimental to the crop and the wider landscape (Howarth, 1990; Potts, 1990). Remember an early (1947) fiasco: the ill-fated 'Ground Nut Scheme' in East Africa, promoted with the best intentions but minimal ecological and local knowledge. The British tax payers paid £36.5 million for this aid (a nice house then cost £500!) at a time when they could least afford it. Of course, there are cases by the legion in which the misuse of insecticides has led to diverse problems (Section **13.2.3.4**), particularly to the creation of new pests and so crop losses.

In **Chapters 9** to **12** we examined the general autecology and population dynamics of insects, biasing our treatment towards pests. The various methods used in the economic control of such pests have been dealt with above, so we are in a position to consider how these inputs might be integrated efficiently. Walter (2003), in a profound book, examines the links between ecology and pest management, a previously grey area. In applying science to IPM there should be two phases: (i) applying scientific understanding, and (ii) applying techniques. He paraphrases Pasteur, 'There are not two kinds of science; there is science and there are the applications of science'. Here we consider both. We are 'now in a renaissance of integrating chemicals and biologicals for sustainable pest control with human safety' (Casida and Quistad, 1998).

At first the use of effective OCs led to the demise of many existing cultural methods (Section **13.1.3**), although as early as 1939 some workers insisted that *biological and chemical control should supplement each other*. WWII interceded, then Ripper (1944) stressed the same message, while Michelbacher and Bacon (1952) said the 'entire entomological picture' must be considered in developing controls. Stern *et al*. (1959), a paper everyone should read for its depth and vision, again promoted integrated control, saying: 'applied pest control … combines and integrates biological and chemical control'. It is an optimized, multi-component approach (Kogan, 1998). Indeed, some apple growers in Nova Scotia had been using, unsung, integrated methods since the 1940s (Whalon and Croft, 1984). Ideally, while chemical methods are temporary, biological ones should be permanent and self-perpetuating. But even temporary results may be beneficial. Ripper (1944) used field fumigation with nicotine vapour against *Brevicoryne brassicae* infesting Brussels sprouts. The method had a strong selective effect, in one field reducing the aphid population of >2 billion/ha by 99.9%. But the *Aphidius* parasitoids (Section **8.2.2.5(m)**) were unaffected, massively improving the ratio of enemy to pest.

The Food and Agriculture Organization (FAO) of the United Nations defines IPM as a system that, 'in the context of the associated environment and population dynamics of the pest species, utilizes all suitable techniques in as compatible a manner as possible and maintains the pest population at levels below that causing economic injury'. We add to this wisdom that IPM is an *endeavour* that does not always keep pests below the EIL, as with *Ostrinia nubilalis* and *Pectinophora gossypiella* (Section **13.2.4.6**). As in the levels of autecological space, IPM can be applied at ascending levels and so grades into CBC. Knipling (1955) advocated pest suppression over wide areas, called total pest management, although his name is usually associated with SMT (Section **11.2.3.8**). If the focal pest is an effective migrant (Drake *et al*., 1995) this would be the only lasting solution. While the EIL is a concept integral with IPM, its link to practice has been questioned (Ehler and Bottrell, 2000). To promote IPM it is best to show its cost effectiveness (Trumble *et al*., 1994, 1997; Burkness and Hutchison, 2008). But legislation against nasty pesticides also helps, while Trumble *et al*. (1994) refer to 'the growing perception that consumers bear the burden of risk when pesticides are used, whereas growers reap the profit'. Not only the growers!

The general aim of IPM, apart from *satisfactory and sustainable* control of the pest, is to reduce widespread contamination (Walter, 2003). Most importantly, this means reducing chemical pollution and hence deleterious effects on our health and on species diversity. Persistent pesticides, especially OCs, have been the main culprits. Where insecticides must be employed, use must be made of their possible differential action on the pest and its enemies, as Ripper (1944) pointed out long ago. For example, many stomach poisons and systemics have few bad effects on enemies, although it is probable that pest resistance to them would occur ultimately. But pesticides are not the only problem. Destroying forests and wetlands to control insects such as mosquitoes and tsetse has been a major factor in reducing biodiversity. Again, the injudicious introduction of biocontrol agents can also lead to extinctions (Pimentel *et al*., 1984; Howarth, 1991; Strong and Pemberton, 2000; Section **13.2.3.6**), especially on islands with unique biotas. Also, research that is integrated with programmes of public awareness is helpful. Wild life television has a large and favourable impact. Also, an aim of secondary education should be to open young minds to the power of logic and science (Walter, 2003). In many places poorly educated people *do not even recognize cause and effect*: *they believe in luck*. Not only do we need scientific advance, we also need a public concerned with such advance and governments ready to promote it.

Essentially, the aim of reducing pest densities runs counter to the basic tenet of evolution by survival of the fittest. Farmers and entomologists strive to create crop environments where the pest's RS is minimized. But pest individuals, placed thereby in deteriorating conditions, are naturally selected to find *every conceivable* way, indeed, some inconceivable ways, out of their predicament. This is a reason why biocontrol in its various forms comes closest to *ideal control*. As pests seek to evolve away from restraints, beneficial agents co-evolve to meet the change. With a fixed chemical control this cannot happen. The change that *does* occur is our tuning the control system, often by increased dose or using a different insecticide. Naturally, the specifics of IPM vary according to *local conditions*. So, in the examples below this must be borne in mind.

The fundamental of IPM is to woo growers away from the collective madness of 'insurance spraying', that is, drenching our environment with herbicides, fungicides and insecticides. Great economy in the use of agro-chemicals is achieved by following the advice of professional services. But even in Dutch IPM apple orchards >50% of the insecticide applied is thought to be redundant (Blommers, 1994). Herbicides and fungicides are often more important in terms of weight. Annual figures for Ireland (O'Brien and Mullins, 2009) give 663 tonnes of herbicide, 619 tonnes of fungicide but only 29 tonnes of insecticide. But one cannot spray *just the crop*. Because of drift, run-off and stream movement (Section **13.2.3.3**) *our locality* is treated. Also, only 30–50% of a nitrogenous fertilizer applied is assimilated by crops, much of the rest runs off, causing eutrophication (q.v.) of rivers. Similarly, phosphorous uptake is small. This is not only pollution but also waste. Ideally, whatever is applied to the field should stay in the field, or be removed at harvest. More methods of reducing such losses, which should be no more time-consuming or costly than spraying, are needed. These include trapping and scouting (regular inspection) and an entomologist to identify pests and their damage. Crops should be sprayed only when necessary. Indeed, IPM is often less costly by reason of reduced chemical use. While good IPM systems may be developed for a given crop there is always a retrograde tendency simply to use a new insecticide and forget the rest of the package. This happened to early IPM of apples in Nova Scotia (Croft and Hoyt, 1983). But the reaction has never worked and my guess is it never will. *Lasting control requires co-evolution* (Section **8.2.1**, above), maybe augmentation of the pest's enemies, and judicious use of safe insecticides.

For plant production we examine IPM in three situations: field, orchard and forest. These are of increasing age and so we expect such ecosystems to have greater faunal diversity as the plant architecture becomes more complex (Lawton, 1983). Plants of simple architecture dominate wheat fields, although a few annual weeds may have survived herbicidal treatment. Heterogeneity is largely horizontal, but in orchards and more so in forests vertical complexity increases (Section **9.5**). In annual field crops, most pests and their enemies, apart from the soil fauna, have found the field during warm weather, often from its margins. But broad-leaved forests are longstanding ecosystems with a rich biota. Also, pests of field crops attack highly productive plants, many of which are derived from early successional stages; in forests they attack mature trees that have passed their peak efficiency (Wallner, 1987). While IPM has been applied mainly to crops, the concept is also applicable to the control of insect vectors of disease. In estimating the densities of insect vectors of human diseases, one must know by experience the critical levels below which transmission becomes trivial (see Section **13.4.1**).

13.3.2 IPM in field ecosystems

13.3.2.1 General introduction

Field crops normally take less than a year from planting to harvest. Following this, for hundreds of years, such crops have been rotated annually to reduce pest populations and promote soil fertility. Even so, many cereal crops are grown continuously: although for wheat this is a recent trend. Rice may alternate with fallow, as in Bali (Walter, 2003), or with vegetables as in Kerala, India, while in the terraced Himalayan foothills of Uttarakhand, rice is grown in the wet season from June to October and wheat during the rest of the year (personal data, Fig. 13.17). Maize, barley, oats, sorghum and millet are the other major grain crops. There is also a variety of longstanding, non-grain field crops including sugar cane, sugar beet, flax, sisal, sunflowers, oilseed rape and pineapples. Cassava and cotton, although bushes, are effectively field crops too.

In the beginning, all field crops were effectively horticultural since the lack of powered equipment allowed only small areas to be cultivated. Nor were large amounts of food necessary for city populations. As noted, there is a continuing trend to grow horticultural crops on an agricultural scale: a trend that can bring a Pandora's Box of attendant woes. Critically, where forest is cleared to grow field crops, wide-scale drying out of the environment ensues, not only because of the enhanced evaporation due to increased temperature and wind speed, but also because there are no trees to trap atmospheric water. But this can be reversed; after afforestation near Khon Kaen, Isaan, Thailand, the local water table rose 6 m in a 10-year period (Freeman, personal data).

In field monocultures the insect's food patch becomes unnaturally large (the size of the field), predictable, rather uniform, effectively a one-patch habitat. Thus, non-migrant, searching pests emerging within it may find food easily and reproduce, so promoting their population growth (Section **12.2.1**). This is especially significant where the searching capacity of the pests is limited, as in *Contarinia* midges and Colorado beetles, less so for mass migrants (Johnson, 1969) like frit flies. Also, since many cereal pests evolved from insects inhabiting extensive grassland, there is no fundamental spatial change for them to adapt to. In continuous cropping the pest's food supply is rather constant, as the logistic model (Section **11.5.2.1**) assumes. Furthermore, a patch with simple architecture may, but often does not, contain food for the pest's enemies. Searching parasitoids need nectar, which is often unavailable or of short duration in field crops, especially where herbicides have been applied, although honeydew will be present if aphids are present.

Traditionally, grain was grown agriculturally and vegetables horticulturally. The new trend to grow vegetables agriculturally has been limited by the rise of 'organic' production, although this may not give a superior product (Trewavas, 2001). Potatoes and peas are now often grown on an agricultural scale. IPM practice on these two scales is different, but with reduced pesticide use agriculture should become more 'organic', founded on ecological principles (Potts, 1990), and its products improved nutritionally, not just in appearance. Pleasing the eye does not enhance their stock of nutrients, another facet of deception (Trivers, 2011) and root crops often contain too much water, limiting shelf life and taste. In short-term field and orchard crops insects operate in an annual sequence in relation to the crop cycle, there being early, mid and late pests. In fields, early damage stunts young plants, but with over-sown cereals this may not have much effect on yield. With rapidly increasing biomass in the mid-term, pests often have the least effect, while late season pests, because they attack the marketable product for which there can be no regrowth, are the most important.

13.3.2.2 The agricultural scale: Wheat and rice: Commonalities and contrasts

Both crops are of great antiquity. Wheat cultivation started in the Fertile Crescent ~10,000 years ago

Fig. 13.17. A terraced landscape in the Himalayan foothills. Source: Wikimedia Commons, author Ramwik.

(Potts, 1990) although rye came 3000 years earlier (Jones, 1999). Presently, the area under wheat is about twice that of rice at ~4 million km^2 and ~2 million km^2, respectively (Leff *et al.*, 2004). Rice growing may have begun in Isaan, Thailand, ~9000 years ago (Bray, 1986); Jones puts its origin at 12,000 years ago in the Yangtze Valley in China. So it has been grown extensively for millennia, by the subtle modification of water sources and the steady efforts of local labour (Fig. 13.18). Even today, ~15% of our global population are subsistence rice farmers, while 60% of us depend on it as a staple food (Teng, 1994; Ives and Settle, 1997). The increasing extent of agriculture in the recent past has had great effects on the spatial relationships of insects and their natural enemies. We recall (Sections **12.3.4.4(d)** and **13.1.2.3**) that local densities of such species, here pests, are strongly influenced by their regional distribution and density (Hanski, 1983; Leather, 1986; Gaston and Lawton, 1988; Cornell and Lawton, 1992). The greater the *regional* area occupied by a crop, the higher the pest density expected *locally* within that region. But such densities are also influenced by crop cultivar and agricultural practice (Kisimoto, 1984).

Wheat to temperate regions is what rice is to India, Pakistan and South-East Asia, that is, the primary grain crop and staple food. European wheat grew traditionally as a phase of rotation that included grassland, legumes and a root crop. Experiments at Rothamsted in the 1800s showed the possibility of growing wheat continuously in the same field. But this was with adequate irrigation and proper husbandry. Conversely, total breakdown of the ecosystem occurred in parts of the American prairies after only a few years of amateur cultivation of maize (Steinbeck, 1939). Unlike wheat fields, rice paddies are a blend of terrestrial and aquatic ecosystems. But due to forest clearance, both cultivations may lead to depleted

Fig. 13.18. Rice paddies in Cambodia.

aquifers (Section **13.3.2.1**). Unlike the rotation of many other field crops, monocropping wheat and rice (Luttrell *et al*., 1994) produces habitats of similar duration to natural grasslands. Apart from insects, cereal crops are afflicted by weeds and pathogens such as *Blumeria graminis* and *Septoria* spp. (glume blotch and leaf spot), *Claviceps purpurea* (ergot), *Puccinia* (rusts of wheat), and *Magnaporthe grisea*, *Thanatephorus cucumeris* (damping-off disease) and *Cochliobolus miyabeanus* (brown spot of rice) (Oerke, 2006).

13.3.2.2(a) WHEAT. The global area in production being vast (~4 million km^2) makes wheat, together with other grain crops, sugar cane and pasture, form effectively a major, grassy, global biome (Section **2.2.3.1**). Yields range from 8.5 t/ha in Ireland (Oerke, 2006) up to 16 t/ha in favourable fields and years in south-east England (Andrew Phizacklea, personal communication), to <0.5 t/ha at Hyderabad, Andhra Pradesh, India (17°N), the southern limit of production. High yields result from *intensification*, larger fields, more agro-chemicals, irrigation and higher bearing varieties (Potts, 1990; Matson *et al*., 1997). There are two wheats, *Triticum aestivum* (bread wheat) and *T. turgidum* (rivet wheat). Numerous cultivars exist both for autumn and spring planting and for producing special flours. Like other cereals, wheats are oversown, so that the death of a young plant allows others to replace it, making these crops tolerant of early damage. For example, a spring attack by *Delia coarctata* (Section **3.2.2.1(j)**) is usually compensated by the enhanced growth of adjacent plants. What must be avoided is loss of developing grain, since it is irreplaceable. This is why aphids such as *Sitobion avenae* and the wheat blossom midges (*Contarinia* and *Sitodiplosis*; Section **6.2.1.2(j)**) attacking the flower heads can be so damaging.

Total losses in wheat production vary from 14% in Western Europe to >25% in many other regions. Insects, including the result of their transmitting pathogens, may contribute about a third of this loss. Wheat has ~10 major and ~60 minor pest insects, but the important part of the pest spectrum varies with time and place (van Emden and Service, 2004; Oerke, 2006). The pest aphids are: *Diuraphis noxia*, *Sitobion avenae*, *Schizaphis graminum*, *Rhopalosiphum padi*, *Metopolophium dirhodum*, *Me. festucae* and *Macrosiphum avenae*. They all transmit viruses (Section **5.3.1.2(h)**). *Frankliniella tritici* (Section **6.3.1.1(g)**) and *Blissus leucopterus* (Section **5.3.1.1(a)**) are further exopterygote pests, and the bug *Eurygaster integriceps* is a pest in Southern and Eastern Europe through to Iran (Potts, 1990; Iranipour *et al*., 2011). *Cephus cinctus* (Section **4.4.1.1(b)**) is a pest in Canada and so is *Oulema melanopa* (Section **5.2.1.2(d)**) in the USA (Altieri, 1990). Diptera form the other major pest group. It includes the midges *Mayetiola destructor* (probably a species complex), *Contarinia* spp., and *Sitodiplosis mosellana* in Canada (Sections **4.4.4** and **6.2.1.2(j)**). Larval chloropid flies such as *Oscinella frit* and *Chlorops taeniopus* (Section **4.4.4**) bore young stems, while more recently those of a similar fly, *Opomyza florum*, are increasingly found in winter wheat. Within the soil, cutworms (Section **3.2.1.2(e)**) are sometimes destructive, for example, *Porosagrotis* in the Colorado and Montana area, while in Europe *Delia coarctata* may be important, boring the base of the stem. Many of these pests also afflict oats, barley, maize and sorghum.

Much work in Europe and North America has been done over the last 20 years on IPM of this crop, a recent review citing 150 papers. Great differences exist in the physical conditions between the two continents and between maritime and central regions. The pests involved tend to be specifically different, although aphids are important throughout. In Europe, the important ones are *Sit. avenae*, *Me. dirhodum*, *Me. festucae* and *R. padi*, while *Sch. graminum* and *D. noxia* (Section **5.3.1.2(g)**) are most damaging in North America (Brewer and Elliott, 2004). In southern Chile where >120,000 ha of wheat are grown, *Sit. avenae* and *M. dirhodum* caused crop losses reaching 20% in the mid-1970s. But the introduction of several of their parasitoids and the release of many coccinellid beetles stemmed the outbreak (Zuniga, 1986, in Altieri, 1990). Sometimes, however, the build-up of coccinellid numbers occurs after that of their aphid prey (Dixon, 1998; Shannag and Obeidat, 2008). They fail to follow Forrest's maxim.

When beetle banks (Section **13.2.4.7**) are established, the loss of productive area this entails is more than compensated by savings on aphidicides. When oilseed rape is grown adjacently, syrphine flies (Section **8.2.2.4(i)**) that feed on the pollen of this early flowering crop penetrate the wheat, suppressing aphid numbers, especially those near the interface. The provision of suitable early flowering plants, such as *Phacelia* (White *et al*., 1995) and oilseed rape itself, provides pollen in beetle banks and may well improve penetration into wheat, as would strip farming of wheat and oilseed rape, so promoting movement of parasitoids. Chambers *et al.* (1982) found that wheat planted in late, rather than early, October, developed lower aphid populations the following June, since the later date allowed little aphid immigration. Under-sowing wheat with clover encourages carabid beetles and improves soil fertility, while under-sowing with grasses provides a winter refuge for aphid parasitoids (Altieri, 1990).

In Europe, and doubtless elsewhere, the timing and dosage levels of insecticides used against aphids are critical (Mann *et al*., 1991). Well-timed, reduced-rate applications maximize profitability. But it is essential that existing natural controls are harmed as little as possible. Polyphagous predators are critical in restraining these pests (Sunderland *et al*., 1987; Winder *et al*., 2005), the former finding that apart from carabid and staphylinid beetles, spiders such as *Erigone* are especially important. In Sweden, *Pardosa* spp. (Lycosidae), *Oedothorax apicatus* and *Erigone atra* (Linyphilidae) and *Pachygnatha degeeri* (Tetragnathidae) are effective predators (Öberg and Ekbom, 2006). Aphidiine parasitoids, in particular, also restrain the numbers of cereal aphids there. In Lower Saxony, Germany, landscape complexity also influences this interaction, a macro-ecological effect (Thies *et al*., 2005; Section **12.3.4.4(d)**). Complex areas had higher levels of colonization by aphids but also higher mortality from these parasitoids. For more data on IPM in wheat, see Wilde (1981) and Wratten and Powell (1990) in Firbank *et al.* (1990).

13.3.2.2(b) RICE. Rice, *Oryza sativa,* cultivation in paddy fields in India and South-East Asia is an ancient practice developed more as an art than as a science. *O. glaberrima* is grown in parts of West Africa. Most rice is consumed within the country of origin. For an annual crop ~6 t/ha is commonly achieved, similar to wheat. In tropical areas where three crops are grown per year, ~9 t/ha can be produced (Kisimoto, 1984). But field trials by International Rice Research Institute (IRRI; see below) have produced twice this yield. Sustainability is usually maintained by the input of dissolved nutrients when the fields are irrigated and/or flooded, as in Isaan, the Mekong Delta, Java and Kerala. A rich biota develops, including many pest enemies and alternative prey, both in the paddies and on their banks. Adding an aquatic environment to the terrestrial one of the banks is the main cultural difference between rice production and that of other cereals. But the tropical location is a further cause of high biodiversity. In some upland and lowland areas of India, Africa and Latin America this crop is fed mainly by seasonal rain.

With the advent of high-yielding varieties (in around 1965), organic pesticides and herbicides, many farmers were to their detriment coerced from tradition. The ecological web was broken, producing 'vacant niches' (Lawton, 1982) for pests. In a 1987 survey in the Philippines, Teng (1994) found no significant differences in yield between fields with and without insecticidal application! In a fine display of spin, some companies referred to their insecticides as 'yield enhancers'. Apart from the suppression of natural enemies by these chemicals, more subtle effects have been documented. Applying insecticides such as jingganmycin and bisultap, and herbicides such as butachlor, *decreases* its resistance to *Nilaparvata lugens* for ~2 weeks (Wu *et al*., 2001, 2004). Some pesticides increase the concentration of amino acids and decrease that of sucrose, thereby promoting an increase in pest numbers (Kisimoto, 1984; White, 1993). Now to promote IMP and greater sustainability, farmers must be wooed away from their addiction to 'quick fix' chemicals (Settle *et al*., 1996; Matteson, 2000). The social environment of rice farmers is far different from that of European and North American wheat growers, and so programmes in agronomy have been instituted in South-East Asia, often under the auspices of the FAO. So, by 1996 more than a million rice farmers there had been exposed to the IPM concept (Kogan, 1998). The IRRI in Luzon, Philippines, founded in 1960, plays a nuclear role in rice farming technology.

Unlike wheat, rice pests are dominated by virus-spreading delphacid bugs, the upsurge of several being the result of spraying pesticides (Teng, 1994; Ooi, 1996). Public enemy number one is usually *Nilaparvata lugens* (Section **5.3.1.2(d)**), while *Sogatella furcifera* may be locally important. Outbreaks in some sub-tropical regions provide huge source populations for summer migrations into China, Korea and Japan (Drake and Gatehouse, 1995). Green rice leaf-hoppers, *Nephotettix* spp. (Section **5.3.1.2(a)**) are similar pests, while *Nezara viridula* may cause local damage. Stem boring by pyralid moths *Scirpophaga incertulas* and *S. innotata* is widespread but usually minor (Section **4.4.1.1(d)**). However, *Chilo suppressalis* is becoming common in thick-stemmed cultivars. But like wheat, rice can compensate for loss of leaf area by munching pests, such as the pyralid leaf folder *Cnaphalocrocis medinalis*, the ephydrid fly *Hydriellia philippina* and the chrysomelid beetles *Oulema oryzae* and *Dicladispa armigera*. Even damage to 50% of leaves at tillering fails to affect the yield. As in wheat, more loss results if attack occurs when grain is developing (Kisimoto, 1984; Bandong and Litsinger, 2005).

IPM in rice paddies depends on conserving a rich biotic environment (Ooi, 1996), essentially a return to tradition, but with modern inputs. So, when paddies are fertilized organically their enhanced fauna of detritivores, especially aquatic insects such as the Chironomidae, conserves many generalist predators that prevent pest upsurge (Settle *et al*., 1996; Section **5.3.1.2(d)**). This occurs early in crop growth, again recalling Forrest's maxim. The dynamics of these predators become decoupled from those of potential pests (Sections **11.5.2.2** and **11.5.2.3**). In such an environment nymphal and adult Odonata check the numbers of malarial mosquitoes, as do a variety of small fishes, and consume the adults of several rice pests. Indeed, landscape-wide planning needs to be undertaken (Settle *et al*., 1996). My view, based on personal experience in Isaan, is that a comprehensive programme of afforestation, widening the banks of the paddies to about 2.5 m, and reshaping fields to have a width no greater than 100 m, are the keys to CBC in rice. Forests conserve species, accumulate water and give additional production. Wide, major banks planted with flowering shrubs and diverse grasses conserve pest enemies and provide them with nectar. Major banks also allow access by vehicles, and minor banks (<1 m wide) allow further penetration of enemies and the control of flowing water. Trees and bananas provide shade for workers, reduce wind speed and so evaporation. *A small decrease in crop area permits a large increase in that under conservation: new green technology gives more rice.*

After all, habitat destruction is the major cause of species extinction (Lande and Shannon, 1996) and adequate habitat area the major factor in conservation (Hanski, 1998b). Modern developments can be dovetailed into traditional practice, especially the use of new rice cultivars. Such plants increase production by improved yield and enhanced resistance to pests. Apart from high-yielding cultivars of the last several decades, new hybrid rice cultivars promise further increases of up to 20% (Matteson, 2000). Types with thicker stems, increased leaf area (where nitrogen is stored) and greater panicle weight are becoming available, with a potential further 25% increase. Rice production can be increased without environmental degradation. The skill of the local farmers, however, is vital (Ooi, 1996). Rice IPM must be a 'three-way-street' with scientists, agronomists and farmers participating with mutual respect. For take-up of new technology the people with sun on their backs and mud at their feet must feel valued participants. After all, the former misuse of insecticides was a 'top-down' error! But the results of Asian Farm Schools (Ooi, 1996) are consistent: *less insecticide, more rice*.

The advent of cultivars having pest resistance has been a priority of new rice biotechnology. Some contain oxalic acid, a feeding inhibitor to *N. lugens*. But cultivars with high asparagine and sucrose levels stimulate feeding rates (Denno and Roderick, 1990), while early resistant varieties, such as IR26 in Indonesia, quickly became ineffective. Genes coding for protease inhibitors toxic to *N. lugens* have been inserted in rice (Lee *et al*., 1999) and breeding *Bt* rice having delta-endotoxins is continuing. Extensive trials in China started in 1997. Japonica cultivars may react to delphacid eggs by forming watery lesions containing the ovicidal compound benzyl benzoate (Seino *et al*., 1996). Planting rice having other toxins confers resistance to endophytic stem borers and exophytic caterpillars. It avoids applying insecticides. Nor do these cultivars affect directly the predatory complex. However, if *Bt* rice is not deployed to avoid the evolution of resistance by pests (Matteson, 2000; Gassmann *et al*., 2009) its useful life span may be reduced.

A recent debate concerns whether or not to plant rice synchronously over adjacent areas (Ives and Settle, 1997). Simple theory predicts that synchrony would break the life cycles of pests in the same way as fallow can do in temperate agriculture. Indeed, we noted above that break crops, such as wheat, grass or vegetables, are grown in various regions. But some comparative statistics from Java and Malaysia show the opposite: planting asynchronously reduces pest activity, probably because, in turn, their natural enemies are more numerous and appear earlier (Ives and Settle, 1997).

13.3.2.3 The agricultural scale: Cotton

This major crop comprises *Gossypium hirsutum* (short staple cotton; Fig. 13.19) and *G. barbadense* (sea island or long staple cotton) (Malvaceae) planted on ~500,000 km^2 (Leff *et al*., 2004). The latter is now grown mainly in North Africa and the Middle East (Smith and Harris, 1994). These species are tetraploids but there are >30 spp. of wild, diploid cottons worldwide, which may serve as alternative food for pests, providing reservoir populations (Section **13.1.2.2**). *Gossypium hirsutum* is the more widely grown, but in both cottons there are many varieties. Cultivation exists from tropical to warm-temperate regions. Main producers are China, USA, India, Pakistan and southern states of former USSR. Mexico, Brazil, Argentina, Peru, Turkey and parts of Africa produce appreciable quantities. Production systems vary due to climate and technology. Australia and Israel run small, efficient operations (Matthews, 1989; Luttrell *et al*., 1994), with over twice the world's average production/ha. Much can be learnt by studying their methods. In Australia, natural enemy conservation is used widely (Deutscher *et al*., 2004, in Grundy, 2007). Cotton farmers compete in world markets in fibres both natural and synthetic. Fibre length and strength are important factors in quality. Current world production is ~25 million tonnes of

Fig. 13.19. Short staple cotton, *Gossypium hirsutum*. Source: Wikimedia Commons, credit to Kimberly Vardeman.

lint but cotton seed, a useful food for livestock, is also produced. More data are available in the annual *Cotton World Statistics*.

There are about a dozen major pests overall, again with regional differences in distribution and impact. Biting pests are *Anthonomus grandis*, *Alabama argillacea* (absent from Australia), *Pectinophora gossypiella,* (only tropical) and *Heliothis* (three species). Another budmoth, *Earias vittella*, occurs in India (Section **6.2.1.2(c)**, **6.2.1.2(g)** and **6.2.1.2(h)**). Sucking pests include *Aphis gossypii*, the *Bemisia tabaci* complex (Section **5.3.1.2(c)**), several Heteroptera (*Dysdercus*, *Lygus* and *Creontiades* spp., *Thrips tabaci* and *Frankliniella* spp. Pests that also attack other crops, include *Agriotes* spp., *Ostrinia nubilalis* (Section **4.4.1.1(d)**), *Spodoptera* spp. and *Trichoplusia ni* (Sections **5.2.1.4(i)** and **5.2.1.4(k)**). *Tetranychus* mites are troublesome in arid regions. A range of enemies feeds on these pests. The parasitoids comprise ichneumonid and braconid wasps, *Trichogramma*, and some tachinid flies. The predators are coccinellid beetles, lacewings (*Chrysoperla*), the bugs *Geocoris, Orius* and *Nabis* and several spiders, whose predatory endeavours should be encouraged. Some omnivorous mirid bugs eat the moths, while releases of *Pristhesancus plagipennis* (Reduviidae) have been tried in Australia. Older nymphs are used, being more tolerant of insecticidal residues. Production costs are the main drawback here, but this could be reduced with cheaper rearing methods and sustaining its populations in the field (Grundy, 2007).

As in rice and apple growing, cotton production systems strikingly illustrate the problems resulting from the overuse of insecticides and irrigation (Luttrell *et al*., 1994; Stone, 1999; Thacker, 2002). For example, mass spraying of OCs (Walter, 2003) caused the emergence of *Heliothis* spp. as major pests. From the 1970s, greener tactics have slowly replaced dependence on insecticides, finally resulting in the IPM used where cotton growing is most productive, as in Australia and California. But growers worldwide still use ~25% of all insecticides produced and spray up to 12 times per crop. In some regions, uninformed people have reverted to basic chemical control. In Uzbekistan, after half a century of irrigation from the Amu Darya and Syr Darya, the Aral Sea's feeder rivers, the entire region has become a salt desert as massively increased evaporation brings salts to the surface (Section **2.2.3.2**). Once the World's fourth largest freshwater body, it has lost 80% of its volume and is now saline. Chemical residues from fertilizers and long-lasting OCs blow in the wind (Stone, 1999). In India and Pakistan, where lint production/ha is low, insecticidal use is still increasing. Salesmen from agro-chemical companies, both with vested economic interests, are not blameless (Thacker, 2002), especially in view of the success of IPM in China, Africa and some other regions. So technological transfer from research worker to farmer is vital to maintain efficiency. The strict observance of a closed season of about 2 months is also critical (Matthews, 1989). While it is cheaper and easier to ratoon cotton than uproot and replant it, the latter method ensures less carry-over of pests between seasons.

In northern China, cotton is intercropped with wheat on ~2 million ha (Landis *et al*., 2000). This reduces damage to young cotton by *Aphis gossypii*, since its enemies from wheat arrive in cotton early enough to restrain pest numbers. Lucerne has long been intercropped with cotton in California to trap *Lygus* bugs (Hokkanen, 1991). Sorghum has been used in a similar way, and in addition promotes increased rates of parasitism by *Trichogramma chilonis* on *Heliothis armigera* (Shelton and Badenes-Perez, 2006). In the Texas Great Plains, 4 m wide alternating strips of wheat and sorghum have worked well in trials (Brewer and Elliott, 2004), because the densities of generalist predators are increased.

Production within the US Cotton Belt illustrates the effects of regional variation on IPM techniques. The Belt stretches from coast to coast, some 4000 km long (Bottrell and Adkisson, 1977). The east is damp and sub-tropical with typically >1500 mm mean annual precipitation (MAP), while the west is semi-arid or Mediterranean with an MAP <500 mm. In the centre, the transitional state of Texas presents many ecological contrasts, from the humid coastal areas to the more arid High Plains. In the east, *Anthonomus grandis*, formerly the major pest of American cotton, is being progressively exterminated (Smith, 1998; Section **6.2.1.2(c)**). Apart from trapping and destroying diapausing adults, particle film technology (Section **13.2.3.5(f)**) with kaolin has been used (Showler, 2002). In much of California and Arizona, this weevil is absent and the irrigated desert valleys are relatively pest free and productive. But whiteflies, especially *Bemisia tabaci*, and *Lygus* bugs cause damage (Luttrell, 1994), although trap cropping them has been used. In central and eastern states, damage by *Heliothis* continues, encouraging a large array of natural enemies. Using GM (expressing Cry1Ac or Cry1F), short season cottons and destroying crop residues have been locally effective (Section **6.2.1.2**(**h**)). Glanded cottons emit 100-fold more synomones attractive to the *Heliothis* parasitoid *Campoletis sonorensis* than non-glanded ones. As with resistant rice cultivars, resistant frego-bract cotton improves the efficacy of natural predators against this moth (Lincoln *et al*., 1971). About 30% of cotton is now transgenic (*Bt*) and grown extensively in the USA, Argentina and China. Cultivars such as Bollgard, Monsanto and St. Louis often completely suppress *H. virescens*, but *H. zea* control may still require some insecticides. Newer transgenic cottons containing both the above toxins are under trial (Siebert *et al*., 2008).

13.3.2.4 The horticultural scale: Brassicas

Foliage (cabbages, kale, savoys, Brussels sprouts) and flowers (broccoli and cauliflower) are the main products, so there is low tolerance of damage to these parts, although affected outside leaves can be discarded. Swedes, mustard and oilseed rape (Fig. 13.20) are exceptions grown agriculturally. Lepidopteran defoliators, especially *Plutella xylostella* and *Pieris* butterflies, are widespread, while *Trichoplusia ni* is troublesome in parts of North America (Burkness and Hutchison, 2008). In many regions any IPM strategy must be compatible with controlling *Plutella*. *Brevicoryne brassicae* is specific to brassicas and is annoying when it gets into the heads of cabbages and savoys, while the polyphagous *Myzus persicae* can overwinter there. Both aphids transmit several viruses. *Thrips tabaci* also causes damage inside cabbages, and may fly in from adjacent fields. Flea beetles are destructive of young plants as they retard growth. Pests in the soil, such as cutworms and wireworms, destroy young seedlings, while *Delia radicum* (Section **3.2.2.1**(**i**)) can stunt quite large plants, especially under dry conditions. *Meligethes* beetles (Nitidulidae) may infest the flowers. *Dasineura brassicae* (Section **6.2.1.2**(**j**)) and *Ceutorhynchus* weevils attack the seed pods.

Fig. 13.20. Oilseed rape grown for canola oil.

Trap cropping is especially useful in managing brassica pests. To encourage syrphine flies, major aphid predators, *Phacelia tanacetifolia,* has been deployed as a field border so providing them with nectar and pollen (White *et al*., 1995). To restrain aphids their enemies must arrive early in numbers, Forrest's maxim again. *Plutella* is a cosmopolitan pest, resistant to many insecticides and causes damage everywhere. In lower latitudes breeding is continuous and after cropping it is essential to eliminate residues. Trap crops of mustard and yellow rocket can be effective if parasitoids such as *Diadegma* build up in them (Badenes-Perez *et al*., 2004). Collards expressing Cry1Ac or Cry1Bt genes to control *Plutella* have been tested. But care must be taken as strains with >200-fold resistance to some Cry1 proteins are known (Gould, 1998). Low mesh fences (Section **13.2.3.5(c)**) and trap cropping may be useful techniques against *Delia radicum*.

In a 4-year randomized block trial in Minnesota (plots were 0.04 and 0.01 ha) on a cabbage crop, Burkness and Hutchison (2008) used regular inspection (scouting) and the 'reduced-risk' insecticides spinosad and indoxacarb. These chemicals are expensive and incur an extra cost, but they achieved improved returns of almost US$1000/ha over a conventional programme. Natural parasitoids were probably less affected by these IPM techniques. Such trials are important in showing growers that IPM really does work. Further improvements might well result from a peripheral trap crop (above). But we also note that trials structured like this one alter the spatial arrangement of the food resource for the pests: the experimental treatments were close together not in widely separated fields.

13.3.3 IPM in orchard ecosystems

13.3.3.1 General introduction

For duration and complexity, orchards are intermediate between forests and fields. The grasses and weeds under the trees provide alternative resources for some orchard pests and their enemies. While olive groves form longstanding monocultures, the trend in top fruit production is to have smaller trees, higher plant density, earlier cropping and more frequent renewal (Fig. 13.21). Thus, apple cultivars on dwarfing rootstocks can be grown at densities of ~2000/ha. Since orchards are planted for fruit, many of the pests covered in Chapter 6 affect them. Individual plants give several crops, and again, the marketable product is the most sensitive to damage (Section **3.2.2.1(d)**). In neither forest nor orchard is crop rotation feasible. But in some cases the distinction between a field crop and an orchard is pretty thin (e.g. cassava, cotton and bananas), but multiple cropping from individual, perennial plants is a robust criterion. This excludes cassava and cotton, but includes bananas and plantains, as the plants are effectively small, perennial clones. Coffee, tea and cocoa are thus 'orchards', although in the tropics it is usual to call them 'plantations'.

13.3.3.2 Apples

Apples are a major fruit crop in all temperate and some Mediterranean regions. The many cultivars derive from the Asian *Malus pumila*, not the wild European crab apple, *M. sylvestris* (Alford, 2007). This woodland tree, however, has reservoir populations of bugs, beetles, flies and caterpillars that affect all parts of orchard trees. Many commercial pests are our own creation, again due to pesticide misuse. While mites are not covered in detail in this book, red spider mite, *Panonychus* (= *Metatetranychus*) *ulmi* and apple rust mite, *Aculus schlechtendali*, became pests as a result of such misuse in Europe. An integrated approach to control apple pests is an essential learnt by bitter experience. Predatory *Typhlodromus* spp. mites (Phytoseiidae) must be conserved. In North America too, *P. ulmi* and *Tetranychus urticae* infest apples (Takabayashi and Dicke, 1996), but natural foliar emissions (Section **2.4.2**) attract the mite *Phytoseiulus persimilis* that eats them. Since apples are the marketable product, even slight damage, like that caused by a probing bug, must be avoided. Fruits must be displayed to buyers in good condition regarding size, colour and absence of blemish. Flavour is less important because you cannot taste them in a supermarket as you can in the civilized environment of a French country market place. Then, damaged apples in storage develop brown rot (*Sclerotinia fructigena*), which can spread widely (Sections **3.2.1.2(a)** and **6.3.1.1(g)**), also affecting pears and plums. As in cotton, there is great regional variation and complexity in pests of apple orchards (Croft and Hoyt, 1983; Blommers, 1994; Thacker, 2002). In Indiana, cicadas are a periodical problem (Hamilton, 1961, in Brown and Gange, 1990), where >70,000 nymphs may be sucking the roots of a single tree. Orchards in Italy and Spain may suffer up to three

Fig. 13.21. A modern apple orchard with small, closely spaced trees. Lombardy poplars are in the background (see Fig. 13.15). Source: Wikimedia Commons, author Nicola Quirico.

generations of tortricid leaf rollers, but in Scandinavia there is only one. Recall the contrast between univoltinism and multivoltinism (Section **13.1.2.1**) and generalize the adage (Section **7.3.2.4(d)**) 'every malarial problem is a local problem' to the present case. A universal IPM programme for a given crop cannot exist, our endeavours must be tailored to suit local conditions and temporal changes in the spectrum of pest species.

There are about a dozen major pests and ~60 minor ones (van Emden and Service, 2004), but again their spectrum of importance varies regionally and with agronomic practice. Several, such as the codling moth, are worldwide. Major pests apart from this moth (and the mites) include the related *Cydia molesta* in the Mediterranean, Japan and parts of North America, and several leaf-rolling tortrix moths. Five of these, *Adoxophyes orana*, *Archips podana*, *Argyrotaenia pulchellana*, *Pandemis heparana* and *P. cerasana* are major regional pests with *Ad. orana* especially important in temperate Europe (Blommers, 1994), while *Arg. velutinana* is widespread in North America (Whalon and Croft, 1984). Another leaf-rolling tortrix, *Epiphyas postvittana*, is a pest of pome fruits in Australia and New Zealand (Danthanarayana, 1983). Winter moths eat young leaves and scar fruits. *Spodoptera littoralis* (Noctuidae), the sawfly *Hoplocampa testudinea* and the apple maggot *Rhagoletis pomonella* are regionally important. In North America and sometimes in Europe, *Phyllonorycter blancardella* (Gracillariidae) mines the leaves. Several bugs, especially the woolly aphid, *Eriosoma lanigerum*, are also significant. Other aphids suck the young leaves and developing fruits. These include rosy apple aphids, *Dysaphis plantaginea*, which is troublesome in Southern Europe, grass/apple aphids, *Rhopalosiphum insertum* and green apple aphids, *Aphis pomi*. In Australia, *Thrips imaginis* can be a major nuisance, but in the isolation of Tasmania there are relatively few pests (MacHardy, 2000).

As above, many of these insects have reservoir populations in apple trees scattered in gardens, disused apple orchards, on wild crab apple trees and escapees, and sometimes on woodland trees. While these places are a goldmine of practical material for a class in horticultural entomology, the migrants from them are a constant problem to the grower (Myers *et al*., 1998b). In British Columbia and elsewhere, disused orchards had to be grubbed up before area-wide attempts at eradicating codling moths could be made. In Kent, a major apple-growing area, orchards are often near woods harbouring winter moths. Apart from crab apples, these places have several other of their food plants (Section **5.2.1.4(g)**). Since the females are flightless, old fashion grease banding the trunks eliminates 'residents'. But young larvae can arrive aerially on silken threads.

In any IPM plan for apples insecticides that afflict bees, which are essential pollinators, must be absent during flowering. Apart from *Apis*, wild bees in *Bombus*, *Osmia* and *Andrena* (Section **8.2.1.1**; Fig. 13.22) are key species (Garibaldi *et al*., 2013; Mallinger and Gratton, 2015). Another factor is loss of apical dominance by apple twig cutters and woolly aphids (see Fig. 4.3). This disrupts the effects of pruning and is more important than losing a few flowers to, say, *Anthonomus pomorum,* since after fruits set a tree naturally excises many fruits, mainly early in development. Indeed, only 6-26% of flowers develop into mature fruits (Stephenson, 1981). But there is a relatively long period of maturation during which protection of one sort or another must be in place. Gruys (1980, in Blommers, 1994) promoted the idea that the key to IPM for European apples was that the choice and delivery of insecticides must conserve the predatory mites that suppress their phytophagous cousins, a rationale S.C. Hoyt had proposed for North America. The discovery that some predatory *Typhlodromus pyri* were resistant to several OPs and carbamates facilitated this scheme. Indeed, there are strains resistant to diazinon and fenitrothion (OPs) and to carbaryl and propoxur (carbamates). So these can be used judiciously. Croft and Jeppson (1970) found similar resistance by *T. occidentalis* in North America, while another phytoseiid predator, *Amblyseius fallacis*, and the ladybird *Stethorus punctum*, had also become very resistant. Recall that biological systems are always in a state of evolutionary flux.

Fig. 13.22. A wild bee (*Andrena melittoides*), an effective pollinator of apples. Source: Wikimedia Commons, author Gideon Pisanty.

In much of Europe, two applications of the insect growth regulator (IGR) fenoxycarb (Section **13.2.3.2**), one before flowering and one shortly after, are necessary to restrain the tortricid complex. They do not deter or afflict pollinators. In Southern Europe, further treatments are needed since tortrix moths have several generations. Fortunately *Bt* preparations, which kill moth larvae selectively, are more effective at higher temperatures. But *C. pomonella* eats them only after entering and damaging the fruit and while a specific granulosis virus (CpGV) has been developed, several applications are necessary. The nematode *Neoaplectana carpocapsae* (Jacques *et al*., 1994) has been used widely to limit codling populations and particle films have been applied. In Canada, attack by these moths and *Rhagoletis pomonella* is limited if a 20 m wide border is sprayed in spring (MacHardy, 2000), so reducing penetration by immigrants. Since the orchard's centre is unsprayed, natural control of aphids, leaf miners and mites is more effective, while 90% less insecticide is required. Trials with SMT to suppress the moths, while successful locally, have not borne fruit. Work in Switzerland (Hausmann *et al*., 2005), however, suggests that the eulophid wasp *Hyssopus pallidus* might be used for biocontrol, having caused up to 60% mortality in diapausing larvae. A nuclear polyhedrosis virus is available against *Ad. orana* (AoNPV).

Mating disruption techniques work in some situations and can suppress tortrix moths (Charmillot, 1989, in Blommers, 1994). But pheromone trapping has complex effects. If it allows better timing of insecticidal application, it is effective. If one trap/hectare is set, five moths/trap indicate that spraying is needed (van Emden and Service, 2004). Pheromone environments may thwart upwind flight by males (Hsu *et al*., 2009). But the question remains, do pheromones attract more individuals from outside the crop than from within it? This occurs in *H. hampei* (Section **6.3.1.1**(**b**)), but of course depends on pest mobility. Enemies may also respond to these pheromones and so be killed. Again, high pheromone levels may signal a high density of females to others and so suppress oviposition. Even so, recent work with the specific sex pheromone, codlemone, is beginning to provide effective control of this moth on 160,000 ha worldwide (Witzgall *et al*., 2008). Then, Irvin *et al*. (1999) in Landis *et al*. (2000) found in New Zealand orchards that planting buckwheat (*Fagopyrum esculentum*) increased the density of the leaf roller parasitoid *Dolichogenidea tasmanica*.

There is little tolerance to *Dysaphis plantaginea*. But spraying with selective, systemic aphidicides such as pirimicarb or thiometon to part of each tree works well and conserves predatory mites. Other aphids are less important because the main damage is from their honeydew. Their numbers are often held down in IPM orchards by a predatory complex including earwigs and coccinellid beetles such as *Exochomus quadripustulatus*. This complex, the parasitoid *Aphelinus mali* and using resistant rootstocks, also suppresses woolly aphids. Having read the above, refer to Section **13.2.4** and see Comstock's method for the control of apple maggots!

13.3.4 IPM in forest ecosystems

13.3.4.1 General introduction

These ecosystems range from little-altered forests to monocultures maximizing economic returns (Perry, 1998). They exist from the Equator to the Polar Circles (Section **2.2.3**). Cropping ranges from simply cutting down and removing desirable timber trees to strip-felling, clear felling and replanting pure stands (Fig. 13.23). Coppicing, for example, with hornbeam and chestnut, in which a crop of poles is taken about every 10 years, is another system of husbandry. Excepting this and where the aim is biomass production, crops are normally taken after long periods. So the forest insect's biotic environment varies with time from stability to periodic destruction and in the former case a gradual increase in canopy height and other seral progressions. From early days, workers (von Hassel, 1925; Voute, 1946) drew attention to the great diversity of insects in natural woodlands as opposed to that in cultivated ones, especially coniferous woodlands. Outbreaking insects are more frequent in monocultures, less so in tropical forests (Janzen, 1981; Nascimento and Proctor, 1994; Nair, 2007). Where outbreaks do occur in these forests, they are more frequent on less complex stands such as mangroves (*Avicennia* and *Sonneratia*), teak plantations, and on pines in Indonesia (Kalshoven, 1953).

Because of high species diversity in natural woodlands, a proportion of all types, tropical and temperate, high and low altitude, dry forest and forest wetland, pressingly need to be conserved with *minimal human interference*. In Thailand one may not build at levels higher than the local wat (temple), so conserving forest. Reducing water resources with drainage ditches or pumping water from aquifers causes major disturbance. Trees can be conserved everywhere and the environment improved with a little thought and much good will. In supermarket car parks, dividers can be planted with a variety of trees to produce a canopy of about 30% of natural woodland. This, with little loss of parking space, enhances aesthetics and gives welcome shade for the vehicles – very welcome in the tropics and attracts shoppers! Parks, the borders of railways and roads are other areas where tree cover should be maximized, so providing corridors for migration. Trees stabilize embankments. A friend who designs golf courses tells me he has had more trees planted than anyone else he knows! Forests are not only engines that absorb carbon dioxide, they also trap and conserve water (see Section **13.3.2.1**). Timber made into quality furniture and fittings becomes a semi-permanent carbon sink.

IPM in forests requires area-wide methods, so the situation is in some ways similar to that for other widespread pests: locusts and rangeland grasshoppers, pests of extensive crops like wheat, maize and cotton, even vectors of human and livestock diseases, like black flies and tsetse. Pests localized within the landscape are more vulnerable, but many are truly widespread. Forest pests often come into this category. Area-wide spraying being

Fig. 13.23. Clear felled pines in Ireland – yet to be replanted.

debarred on the grounds of pollution and cost, trapping and intrusive methods of biocontrol, CBC and SMT must be considered, while bottom-up modifications could improve the resistance of trees.

13.3.4.2 North American conifers

Conifers form a natural biome between north temperate hardwoods and Arctic tundra (Section **2.2.3.2**). This vast band of taiga in Eurasia continues across Canada at roughly 50–65°N. Conifers are also present on mountain ranges, tropical highlands and Mediterranean coasts. The biome is hardly represented in the Southern Hemisphere as little landmass exists between 50°S and 65°S, just the tip of South America. Although most pests are regional, the areas involved are almost as extensive as they are for locusts and often also inaccessible. Thus in the 1950s, an outbreak of *Choristoneura fumiferanae* in North America affected 20 million ha of forest (see Fig. 5.4). We confine our discussion here to North American coniferous ecosystems as the information is accessible and has been used in many studies on insect populations. While most of these forests are still original, especially to the north, some have been clear felled and replanted with species we prefer.

Apart from the adelgids (*Adelges abietis, A. tsugae*, *A. piceae*; Section **4.3.3** and Fig. 4.4) and aphids in *Elatobium* and *Cinara* (Section **5.3.1.2**(**h**)) that attack and kill conifers, these forest pests fall into two major groups: wood borers, largely beetles (see **Chapter 4**), and defoliators, mainly symphytan and lepidopteran caterpillars (see **Chapter 5**). Many of the latter came from Europe, leaving their enemies behind and forming outbreaks (Hunter, 1991). They include the moths *C. fumiferana* on spruces and balsam firs and the less important *Lambdina fiscellaria* on hemlock, spruce and firs. The sawfly *Pristiphora erichsonii* infests larch. All diprionid sawflies attack conifers (Price *et al*., 2005). *Neodiprion sertifer, N. pinetum* and *N. leccontei* affect pines and *Gilpinia hercyniae* attacks spruce, of which it has destroyed large tracts. When interactions between folivores and borers exist the latter gain from the tree's weakened defences, but both can cause severe economic losses.

To control defoliators on a forest scale, insecticides were sprayed from the air (Prebble, 1975), an expensive and dangerous adventure doubtless catastrophic to wild life. Hence, control now centres on two methods:

1. Biocontrol is intrinsically attractive, penetrating inaccessible forests (*intrusive*), relatively cheap, and hopefully permanent. Moreover, its delay in coming into effect is less material in a long-term crop. These methods employ insectivorous birds and mammals, parasitic insects and micro-organisms.
2. Mating disruption techniques (*species specific*) with synthetic sex pheromones can be applied from the air and, while not intrusive, affect only target insects. Irrigation is a further possibility. Trees in drought have weakened defences and so where topography and water supply permit irrigation not only improves their resistance to attack but also enhances their growth. Further, it would increase the diversity of all insects, and in turn avian insectivores, and might well give greater ecosystem stability (see below for bark beetles). Dead and dying trees are foci of attack so their elimination, for example by chipping, is important and would provide another saleable product.

For biocontrol, many sawflies succumb to viruses, while several small mammals, particularly shrews, consume their pupae. The voracious *Sorex cinereus* eats large numbers of *Pristiphora* pupae, and without doubt those of most other sawflies and moths in the soil. Shrews are territorial, very active, have higher MR than rodents of the same size (Macdonald, 1984), and consume food, including pupae, at a greater rate (Fig. 13.24). So they are the small mammals of choice for biocontrol. Many parulid warblers, returning from wintertime tropical retreats, consume caterpillars avidly while nesting in spring and feeding chicks. Woodpeckers, especially *Dendrocopus*, eat bark beetles such as *Dendroctonus* spp. directly but may also greatly improve the efficiency of their parasitoids. These methods call for mammalogists, ornithologists and entomologists to talk. Thus, small mammals may benefit from enhanced winter refuges and birds from extra breeding sites.

Parasitoids affecting defoliators are largely ichneumonid and braconid wasps and tachinid flies. *Pristiphora* has been controlled using *Mesoleius tenthredinis* and *Olesicampe benefactor* (Ichneumonidae), while others, such as *Glypta fumiferanae* and *Horogenes conodor*, attack *Choristoneura* larvae and *Meteorus trachynotus* (Braconidae) its pupae. Since their action is inversely density dependent they fail to limit ongoing outbreaks; conversely, they may *prevent* outbreaks from occurring. These indeed are infrequent but severe in this moth. In such a scenario the Southwood/Comins model (Section **11.2.2.5**) should be brought to mind. Larval tachinid flies, such as *Bessa harveyi* and *Drino* spp., destroy sawflies, while *Lypha*, *Phryxe* and *Winthemia* afflict the moths. If more were known of the behaviour and dynamics of parasitoids (Force, 1974; Freeman and Ittyeipe, 1993) it might be feasible to improve their impact on a forest-wide scale, rather in the manner of the CBC concept

Fig. 13.24. *Sorex minutus*, an efficient predator of a wide variety of insects and other invertebrates in forest soils. Source: Wikimedia Commons, uploaded by Salix.

Boring beetles, especially Scolytidae (Section **4.2.1.2**(**f**)), form the other major group of coniferous forest pests and show ecological similarities to and differences from the defoliators. While the adults do not have the great dispersive capabilities of moths like *Choristoneura*, they probably live longer and employ assembly and other pheromones to locate local resources effectively, which is true for some Jamaican species (Garraway and Freeman, 1981, 1990). The genera *Dendroctonus*, *Ips* and some *Scolytus* specialize on conifers, although many bark beetles attack broad-leaved trees. They transmit several pathogenic fungi. Headway in biocontrol is being made using *Rhizophagus grandis* (Rhizophagidae) and *Thanasimus undatulus* (Cleridae) (Ross and Wallin, 2008). *Dendroctonus micans* is vulnerable to attack by *R. grandis* and *D. frontalis* to *T. dubius*. More research is needed on predatory insects affecting bark beetles as the cost of scolytid depredations is colossal. We noted in Section **4.2.1.2(g)** and above that individual trees vary in their susceptibility to attack (Raffa and Berryman, 1987). So apart from top-down biocontrol we might employ bottom-up means to improve the defences of trees, by irrigation, fertilization, by using synthetic anti-aggregation pheromones, even GM.

Two other big groups of boring beetles are the Buprestidae and the Cerambycidae (Sections **4.2.1.2(b)**, **4.2.1.2(d)** and **4.2.1.2(e)**). Many of the former bore broad-leaved trees but a few, like *Melanophila*, prefer conifers. The Cerambycidae has many species of commercial interest by afflicting conifers, especially because, like *Monochamus* spp., they transmit the pine wilt nematode *Bursaphelenchus xylophilus* (Togashi, 1990). This is endemic to North America. So as with bark beetles, much work on biocontrol is needed. A candidate predator is *Trogossita japonica* (Rhizophagidae), which attacks boring beetles, including *Monochamus* spp., in Japan. Then, larval *Cucujus* and *Catogenus* (Cucujidae) are predatory or ectoparasitic on cerambycid pupae. Where pests occur conspicuously and on a macro-scale, as in the present case, satellite imaging is a useful tool to locate them. Defoliating caterpillars may be found in this way and the extent of their damage estimated, the latter being necessary information in planning a response.

13.3.5 Difficulties with IPM and the potential for its improvement

While the efficiency of IPM can be hard to estimate (Walter, 2003), the major problem is the lack of uptake by farmers, a very conservative group. Is this simply inertia or are other pressures at work? Uptake is a lesser problem in organic horticulture. Some studies show that IPM can increase production by >10% (Trumble *et al*., 1994, 1997; Burkness and Hutchison, 2008; Radcliffe *et al*., 2008), translating into a larger profit margin if costs are similar. This aside, crop failures entailing greater financial loss can be averted. Production goals for foods and fibres change with the needs of society and influence IPM strategy, as do more efficient methods. And regional differences in the pest fauna and in crop cultivars must be appreciated. So while IPM is a continuing process, the relationship between research, application technology and uptake needs further development (Walter, 2003), while ecological theory and IPM practice must be integrated more effectively.

I have promoted insect autecology on a more structured basis than formerly and explored briefly the ways it may in restructured form be used to improve the control of pest insects. In particular, people engaged in IPM planning must understand the spatial aspects of insect population dynamics much better than they often do at present (Drake and Gatehouse, 1995; Ives and Settle, 1996). In **Chapter 12** I reorganized the spatial aspects of resource bases and the dynamics of insect populations within and between the various levels. But we must remember that science does not make decisions concerning commerce, they are made in relation to economic imperatives. IPM has many components: scientific, social and economic and with its potential to merge into CBC, also aesthetic ones. Walter (2003) discusses another problem in the theoretical roots of IPM, namely the use of pure demography versus autecology. Recall another dichotomy in Section **11.5**, where marginalization of the physical environment and the absence of spatial effects occur in a whole section of theoretical models. My view is that field autecology as a whole is the proper underpinning to demography and in train to IPM.

13.4 Medical and Veterinary Entomology

13.4.1 Medical entomology

The larger part of medical entomology concerns the transmission by piercing and sucking insects, especially Diptera, of pathogens causing human disease (Sections **1.4.1** and **7.3.2.3**). The various forms of malaria, filariasis, trypanosomiasis, leishmaniasis and numerous arboviral diseases annually afflict millions of people. They kill and cause suffering, loss of fulfilment, production and earnings. Formerly, flea-borne plague and louse-borne typhus caused lethal epidemics in temperate regions but now insect-borne diseases are largely tropical. Direct attack by insects such as mosquitoes, black flies, tabanid flies and even human bots, while irritating, is minor by comparison, but control of all of them follows similar principles. We must: (i) limit their populations; and (ii) prevent or reduce their biting us. As many of these flies are associated with water, limiting its accessibility to them is a prime concern. But this presents a dilemma. Water is often needed to irrigate crops, especially in the tropics, but it also increases the carrying capacity of the landscape for dipteran vectors (Pennisi, 2001; Section **7.3.2.4**(**c**)). Keeping urban environments free from potential breeding sites in human rubbish is a problem that must be tackled at the levels of primary education and governmental legislation. Catching dengue fever is not just a matter of bad luck, it is largely a result of allowing ones immediate environment to promote breeding of *Aedes* mosquitoes. Of course, the efficiency of one's immune system is another factor.

Mixed epidemiological/entomological models have been proposed (cf. Section **11.5**) that can assist us to determine the level of biting below which transmission should become trivial. Apart from their intrinsic scientific value, the main use of predictive models is to make correct choices between different control options, meaning the latter function is comparative, not absolute (Dye, 1992; Section **9.2**). But as in plant protection, greater use of the autecological approach should be made, and this is particularly germane when species complexes are being unravelled. Ronald Ross, as early as 1904, started demographic models, but they were little developed until the 1950s. Macdonald (1957) and Garrett-Jones (1964) proposed two equations that purport to define the transmission to a vertebrate of a disease carried by an insect vector. Essentially, this is a tritrophic situation (Sections **9.1** and **11.5.2.3**). These equations estimate two parameters: the *basic case reproductive number* (R_o) and the *vectorial capacity* (C):

$$R_o = ma^2bp^n / -r\ln p$$

$$C = ma^2bp^n / -\ln p$$

In a susceptible human population, R_o is the mean number of secondary cases arising from each primary one, while C is the daily rate at which future inoculations arise from a currently infective case (Dye, 1992). Here ma is the human biting rate, a the human biting habit, b the proportion of infective vectors that transmit the pathogen to uninfected persons, and $p^n / -\ln p$ a factor describing vector longevity. Here p is its daily survival rate and n the number of days between infection of the vector and its becoming competent to infect, the *latent period*. The parasite's duration of life within people is given by r, the mean daily rate of recovery of an infectious case, this being the only factor that differs in the two equations.

But there are problems in estimating R_o and C, which Dye reviews. An uninfected vector biting an infected person might not pick up the pathogen (Garrett-Jones, 1964), either because its blood meal was small in relation to the intensity of the pathogen or because of the vector's natural resistance to it. This brings the idea of individual variability (Wellington, 1957; Łomniki, 1978, 1988; Bolnick *et al*., 2003) of the host, the parasite and the vector, into consideration. Indeed, vectors may prefer to bite infected hosts (Kingsolver, 1987), which suggests that their behaviour has been moulded by the pathogen, for it is often to the vector's detriment (Dye, 1992; Hogg and Hurd, 1997; Marrelli *et al*., 2007; Section **7.3.2.4**(**d**)). Vectorial capacity is especially sensitive to the vector's survival, which can be estimated by mark/recapture methods (Jolly, 1965; Southwood and Henderson, 2000) although these too are subject to error. Then one could use the *parous rate,* the proportion of female vectors that have laid eggs, but this method is also fraught with inaccuracy as it assumes that their survival rate is not age dependent and that the different age classes are sampled with equal efficiency. Then the vector may well have cyclical behaviour in relation to feeding and reproduction (the gonadotrophic cycle), while the pathogen may reduce the activity and/or survival of the vector (Molyneux and Jefferies, 1986).

However, the *mean number of bites a person gets per day* is generally a robust parameter in epidemiological work and should correlate with other estimates of the numbers of vectors, such as catches in traps (Dye, 1992). Indeed, $R_o \approx 1/x^*$, where x^* is the equilibrium fraction of susceptible hosts. Another approximation in anthroponotic infections is $R_o \approx \lambda L$, in which λ is the per capita rate at which infection is acquired in unit time and L is the host's life expectancy. We must also consider the 'dose' of pathogens transmitted. Great numbers may overcome the host's immune system more effectively. Hence, a simplistic approach may be better. Indeed, Olson *et al.* (1979) in California found a close correlation between light trap catches of female *Culex tarsalis* and the incidence of St Louis encephalitis and western equine encephalitis (Section **7.3.2.4**(**f**)) in human subjects.

Daily survival of individual vectors differs considerably between species in genera such as *Anopheles* and *Glossina*, but more so between more separate taxa such as triatomine bugs and phlebotomine flies. Then, temperature not only effects the survival of vectors but also the duration of the *latent period* of parasite development within them (Section **7.3.2.4(d)**). Another variable is the proportion of a vector species that carries the infective stage of the parasite. It may be <0.1% in tsetse and phlebotomine flies (Lainson, personal communication) but >10% in *Anopheles gambiae* s.l. Even if the proportion of infective vectors is low, disease transmission can still be appreciable if one gets many bites. In parts of Africa, anopheline vectorial density must be reduced 1000-fold before transmission would be interrupted (van Emden and Service, 2004). Bailey (1982) gives a fine early account of models of disease transmission, and Grassly and Fraser (2008) present a recent review.

While IPM usually refers to crop protection, similar methods can and have been applied usefully in medical and veterinary entomology. Indeed, the definitions of IPM (Section **13.3.1**) apply equally to area-wide methods of vector control. So extensive, intrusive methods are *de rigueur* for the effective reduction of vector density. For *Aedes aegypti* (Section **7.3.2.4(e)**), elimination of breeding sites and fogging to destroy infectious adults have long been used. For tsetse, habitat destruction was a traditional method, but increasingly efficient traps are now being developed and deployed. Genetic modification of mosquitoes, again hopefully intrusive and discussed from the time of Curtis (1976), is now under continuing investigation (Ito *et al.*, 2002; Burt, 2003; Marrelli *et al.*, 2007; Yakob *et al.*, 2008).

13.4.2 Veterinary entomology

Pasturing cattle and sheep is sustainable as long as there is adequate water and over-grazing is avoided. But the flow of energy and nutrients within pasture soil, arriving as phytodetritus and coprodetritus, is generally far greater than that above ground (Odum, 1971; Stanton, 1988; Polis and Strong, 1996). And plant production below ground is often more than that above it. Although livestock make a major contribution to energy flow, they represent only part of it. Even so, where they are dense supplementary food is often necessary, but for cattle at least those fed on grass alone produce the best quality meat (Faulkner, personal communication, 2008). Different husbandry results in different livestock density, which in turn affects disease transmission. For example, in dairy farms, cows are brought in for milking twice daily and in cool temperate regions various concentrations of livestock result from fencing them off onto sections of the pasture, and from sheltering them in winter. In such high-density situations, ectoparasites such as lice (Sections **7.2.1.1** and **7.2.1.2**) and ticks may spread, but are more easily controlled than on rangeland. In temperate winters it is too cold outside for biting flies to be active, whose depredations and diseases they may transmit are confined to summer. In winter disease transmission in byres is possible, but with proper husbandry flies are controlled easily. With lax husbandry, however, flies such as *Haematopota* may emerge in cattle sheds in winter and bite the livestock. In the tropics flies are active continuously (Section **7.1**).

13.5 The Economics of Pest Control

Just a few points to conclude. Many of the basic tenets of economics and ecology are at variance. Fundamentally, while profit must increase by at least a modest annual percentage, this is none the less an exponential. On the other hand, ecological processes depend ultimately on the input of energy from the sun and the recycling of elements. This applies to renewable resources that economists refer to simply as '*land*'. Unless they are overexploited their supply is relatively stable or mildly cyclical, not exponential. Non-renewable resources are simply depleted although much is undiscovered. Notice that this rationale can be compared to that given in Malthus' essay on population (Section **11.1.2**): human population potentially increasing exponentially, but the food supply rising only linearly. But not all wealth is created from resources: renewable or non-renewable and monetary devaluation must also be factored in. Division of labour, communication and transport of goods also play basic roles in increasing wealth (Heathfield and Russell, 1992).

Another basic point of variance is that while species specificity is usually a desirable feature of any control method, such strategies are often too limited to be economically viable. In capitalist societies, desirable as they are in many respects, financial considerations become overriding. Hence, research funding is often tailor-made to the needs of accounting rather than to the needs of human enquiry, with consequent waste of money! The long-term ownership of agricultural land has made for the greatest efficiency. Indeed, there has been a natural selection of farmers, a selection in which the currency is monetary, not genetic.

13.5.1 Tropical situations

In the tropics, subsistence farmers commonly plant a variety of crop plants near their dwellings resulting in small, partially isolated patches for any pest insect to exploit. Hence, on a scale measured in hectares, crops are varied and interspersed with many indigenous plants and weeds. This is essentially a horticultural situation in which there should be a high level of human attention on the crop patches, and hence cultural practices, such as hand picking the pests and destruction of the infected plants, should lead to effective pest control, albeit with the occasional use of insecticides. Unfortunately, high tropical temperatures are not conducive to human diligence, and this, coupled with a lack of knowledge of the pests, often leads to quite the opposite outcome. Here, the prime needs are good public health and education in the principle of *cause and effect* before any strides forward in economic entomology can be made. We should also note that the destruction of trees through negligence and necessity is usually the most telling environmental modification, leading, of course, to raised ambient temperatures, rates of evaporation and an increased risk of fire. This sequence of events may culminate in the formation of semi-desert, or what in Jamaica is aptly termed 'ruinate'.

The cultivation of coffee in tropical highlands is a situation in which there is a moderate alteration of the existing forest environment, given that coffee is a tropical understory plant. While it is true that high-altitude coffee may give greater yields when unshaded, this is not true in plantations below 1000 m. Moreover, monocultured coffee pose a considerable long-term risk to the environment, especially at high altitude where slopes are often steep and the rainfall considerable. In the Blue Mountains of Jamaica, famous for quality coffee, total clearance of the indigenous forest to plant *Coffea arabica* in monoculture risks, and has caused, massive erosion of soil during exceptionally heavy rains. A daily precipitation in excess of 20 cm occurs perhaps once every 20 years, causing extensive mud slides on steep slopes where the roots of large trees do not anchor the soil to the shale bedrock effectively. As an example, in a 10-day period in September 2002, >60 cm of rain, associated with tropical storms Isolde and Lili, fell in the Blue Mountains, causing extensive damage. We should also note that some specific areas, which can be defined in terms of their geology, are especially prone to landslides. Maintaining a partial canopy of indigenous trees is a worthwhile insurance. Once the top soil is lost, replacement would take millennia. Also note that large *indigenous* trees are much better able to resist hurricane force winds which often accompany such rains than are any introduced species, as they have been naturally selected to do so, and their presence does much to protect the crop from wind damage. Similar situations apply to many coffee-growing regions of Central America and Colombia.

A great deal of Blue Mountain Coffee, however, is grown in relatively small (1 ha) groves with an admixture of fruit-bearing trees such as breadfruit and citrus, and lower down mango and bananas, along with self-set indigenous trees. Here we have a moderately modified agro-ecosystem often with copious weeds and perhaps some vegetables such as tomatoes, string beans, aubergine and maize.

13.5.2 Temperate situations

The growing of oak in Western Europe was formerly of much greater importance than it is today. Not only was oak famously used in the construction of sailing ships ('Hearts of oak are our ships, etc') but also as the main support in timber frame houses. Oak forests financed by the Royal Navy in Britain were maintained near to the coasts. *Quercus rober* and *Q. pedunculata* are the dominant trees in oak woodland associations. Silvicultural practices aim at producing the maximum of high-grade timber (straight trunks) in the shortest possible time. To this end, seedlings are planted closer together than they would be naturally and a 'natural selection' of the stronger individuals, a process described in forests by Patrick Matthews in 1831 (i.e. before Charles Darwin), allowed to take place. It is well known, however, that slow growth in trees promotes the formation of stronger wood. Because of the long-term nature of the crop, there is little regular interference of what is essentially a natural forest ecosystem, in particular no regular use of insecticides, despite the fact that oak is consumed by a wide variety of insects. Indeed, it is rare to see an oak tree heavily defoliated.

Glossary

There are many technical words in biology, but different workers often use different words for the same thing. While we need new terms for developments, we should try to eliminate duplication by using the word or description that has brevity, clarity and similar meaning in general English. Indeed, I have coined a few new terms in this book (Fisher's Fork, the Williams' effect, ISC = individual searching capability), thus drawing attention to important principles. I have avoided the present fashion, however, of contracting words that are properly hyphenated since it produces ugly and sometimes ambiguous diphthongs and curious words (e.g. microenvironment, pre-existing, preadult; predate, covary, non-insect).

Absolute humidity. The amount of water vapour in the air expressed in gm/m^3. (q.v. relative humidity)
Abundant. Following general English the term is used here to mean having large numbers.
Acidic soils. The pH scale is a logarithmic one that measures the concentration of hydrogen ions. Soils with a pH of <7.0 are acidic and often poor in nutrients (q.v. basic soils).
Adaptive landscape. The fitness of organisms, following Sewell Wright, is depicted as a topographical map. Those with genotypes best able to exploit particular niches (q.v.) form adaptive peaks, those that do not form the valleys. While useful, the concept has been the focus of much scrutiny.
Additive genetic variance. If all individuals were genetically identical for a trait then there could be no possibility of evolutionary change in that trait. Fisher's fundamental theorem states (see Price, 1972) that such a possibility is proportional to the genetic variance at the locus or loci coding for the trait in question and additive because it relates to the sum of all the genes involved (q.v. non-additive genetic variance).
Adiabatic lapse rate. The rate at which atmospheric temperature falls in relation to increasing altitude. It averages 9.8°C/km.
Advanced insects. Those that taxonomists place at the top of classifications. For example, blow flies, with their short body form and reduced wing venation, are more advanced than long-bodied crane flies. However, this does not preclude behavioural and physiological sophistication at any stage. The counter argument is that since all extant, comparable types have been tested by natural selection for exactly the same time since arising from an ancestral form, there can be no objective criterion to distinguish them (Mallet, 2009). But of course, abundance is an additional criterion.
Advection. Global, lateral movement of air or water masses.
Adversity selection. A principle due to Greenslade (1983) that in addition to *r*- and *K*-selection (q.v.) a further selective mode exists in relation to harsh environments (q.v.).
Aerosols. Small salt or dust particles in the atmosphere.
Aetiology. The scientific study of causation, a term used frequently in pathology.
Age distribution. The statistical, frequency distribution of age classes in a population.
Age-specific fecundity or mortality. The mean number of offspring produced or the risk of death per unit time for a given age class.
Agro-ecosystem. The crop environment, a term drawing attention to the fact that ecological processes still have the upper hand in farming.
Agro-forestry. The application of agricultural practices to the production of trees.
Agronomy. The application of science to crop production.
Aestivation. Passing the summer in an inert phase, often diapause (q.v.).
Aggregative response. Of enemies that move so aggregating within populations of their victims.
Alate. Possessing wings.
Albedo. The reflectivity of the Earth's surface or clouds.

Allee effect. The principle that numbers or population densities below a given threshold are disadvantageous to an individual's reproductive success (= RS, q.v.).

Allele. One of a set of alternative forms of a gene which may be present at a locus.

Allomone. An airborne chemical messenger, other than a pheromone (q.v.) in which the transmitter benefits, e.g. one repelling an enemy.

Allopatric. Of populations or species with separate and disjunct spatial distributions.

Alpha diversity. The diversity of organisms at a location, often within a plant community.

Altruism. Of acts that benefit the recipient at some cost to the actor.

Anabatic. Of winds resulting from the upward movement of heated air.

Anemophily. Wind pollination.

Anemotaxis. Directed movement of an insect in relation to the wind.

Angiosperms. Flowering plants, comprising some 250,000 species.

Anthroponosis. Transmission of pathogens that, apart from the vector (q.v.), involve only human populations (e.g. **onchocerciasis**).

Antibody. An immunoglobulin protein in the serum that binds with a specific antigen (q.v.), thus preventing the latter from having further activity.

Antigen. A substance that causes the production of antibodies.

Antixenosis. Of plant defences that totally inhibit feeding by a herbivore.

Aposematic. Of animal colours that have a warning function.

Apparency. A term including both spatial extent (biomass, q.v.) and duration of a plant or part of a plant.

Apparent mortality. In a life table (q.v.) the number of individuals dying within a stage as a proportion of the l_x (q.v.; see Section **11.4.3**)

Appetitive movement. Locomotion functioning to seek resources or mates.

A priori. Of reasoning before an event.

Apterous. Without wings.

Arbovirus. A word derived from 'arthropod borne virus'.

Arms race. The co-evolution (q.v.) of mutual counteractions between a victim and its enemies.

Assortative mating. Mating between like individuals, there being generally an underlying genetic basis. (q.v. inbreeding)

Autecology. That branch of ecology concerning single species.

Autogenous (opp. anautogenous). Of biting female flies that produce eggs without first taking a blood meal.

Autosome. A typical chromosome; not a sex chromosome.

Autotroph. Plants: the term means self-feeding. Terrestrial plants grow by producing organic materials from gaseous carbon dioxide, water and minerals from the soil.

Axial tilt (= obliquity). The angle, presently 23.3°, at which the Earth rotates relative to the Sun's incident radiation.

Axiom. An incontrovertible fact: e.g. populations do not increase without limit; q.v. postulate and see Section **11.5.1**.

Bacilli. Rod-shaped bacteria.

Baculovirus. A virus from the Baculoviridae, a family found only in arthropods and hence regarded as innocuous to other organisms. The suffix '*-viridae*' is used for all families of viruses.

Baker's rule. The principle that self-fertilizing plants are better colonists of distant areas because a single individual can then propagate itself. It relates to an Allee effect (q.v.).

Balancing selection. Selection that maintains a balanced polymorphism in a population.

Barriers to interspecific mating. Arising from the Wallace effect (q.v.), it is generally held that sympatric and parapatric incipient species will evolve mechanisms to avoid the production of unfit hybrids. Such barriers may operate wastefully after the production of the zygote (post-zygotic mechanisms) or more efficiently prior to fertilization (prezygotic mechanisms). An alternative, but to my mind an additional, theory regards speciation as a result of the development of mate-specific recognition systems (q.v.).

Basic soils. Alkaline soils with pH >7.0. They are typically rich in nutrients.

Batesian mimicry. The relationship in which a harmless mimic evolves increasingly to resemble a harmful model. An example of natural deception originally described by Bates.

Beta diversity. The rate of change of organic diversity along a geographical transect Section (**2.1**).

Biocoenology. The scientific study of living communities.

Biofacies. In biology, the biological characteristic of a species. In palaeontology, a set of rocks possessing a distinctive suite of fossils.

Biogeography. The scientific study of the geographical distributions of species.

Biological amplification. Of pathogens reproducing and increasing their numbers in alternative host species.

Biological species. Groups of actually or potentially interbreeding organisms that in nature are genetically isolated from other such groups. In the insects in particular, a large majority of species were named initially on the basis of adult morphology alone (Linnaean species). While a good correlation exists between morphological species (q.v.) and biological species, one must be aware that searching ecological studies often reveal sibling species (q.v.).

Biomass. The mass of living material either for a focal species (q.v.) or for any multispecific association.

Biome (= global association). The largest community unit that is convenient to recognize on land.

Biosphere. That part of the Earth capable of supporting life.

Biota. Living organisms.

Biotic (opp. Abiotic). Relating to life. We include here recently dead organisms (necron, q.v.) as well as actually living ones (see Section **9.1.7**).

Bottleneck effects. If a population has passed through a period of low numbers, it has likely lost some of its genetic variation, particularly that due to alleles that are rare.

Bottom-up effects. In autecology, factors acting on focal individuals from lower down in the food chain (q.v. top-down effects).

Brachypterous. Having short wings.

Bulb. A storage organ comparable to a corm (q.v.) largely comprised of adpressed leaves attached to a disc-like basal stem.

C_3 and C_4 plants. These are angiosperms with different metabolic pathways that have evolved many times in both dicots and monocots. Only C_4 plants concentrate CO_2 in special bundle sheath cells, permitting high photosynthetic yields and negligible photorespiration, which compromises photosynthesis in C_3 plants. The initial product is a four-carbon molecule such as malate, hence 'C_4'.

Cambium. The generative tissue distant from the tip in a plant stem.

Cannibalism. Intraspecific predation.

Carrying capacity (*K*). The maximum number of individuals that can be sustained throughout their life cycle by the resources of a defined area. Since the level of resources may vary, so may *K*. The term is usually applied to populations (q.v.).

Catastrophe. In ecological terms this is a *local event* of such severity as to kill everything within its ambit.

Cephalic. Pertaining to the head. Since it is derived from the Greek word '*kephale*' it ought to be pronounced with a hard 'c', but often is not.

Cf. (confer). Compare.

Chaos (adj. Chaotic). Disorder. In Greek mythology the most ancient of the gods, in Christian lore the state of the Universe before it was brought to order by the Creator ('… the vast immeasurable abyss, Outrageous as a sea, dark, wasteful, wild.' – Milton. But in population dynamics it refers to *a sensitive dependence on the initial conditions*. Chaotic systems are 'noise amplifiers' that magnify perturbations (Ellner and Turchin, 1995).

Chorion. The shell of an insect's egg. It may be remarkably complex (Hinton, 1981).

Chromosomal inversion. A modification of part of a chromosome in which the sequence of genes is reversed. Inversions serve to conserve sets of co-adapted genes and are well studied in natural populations of *Drosophila* and *Anopheles*.

Clade. A monophyletic group of taxa. They are more related mutually than they are to members of other clades.

Climate. The long-term average of weather in a given area.

Climax community. The sere (q.v.) that ultimately develops in a given locality.

Cline. A gradual change in the characteristics of a species over a geographical distance.

Clone. A group of organisms with identical genetic structure, normally arising by asexual reproduction from an ortet (q.v.).

Co-evolution. An evolutionary change in a trait (q.v.) in the individuals of one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first (Janzen, 1980). Co-evolution must be *continuing* and *reciprocal*.

Cohort. A group of conspecific organisms that hatches at the same time and place.

Common (opp. rare). May mean numerous relative to resources (Andrewartha and Birch, 1954) or, more loosely, frequently encountered.

Competition. The endeavour of two or more individual organisms to obtain that measure of a necessary resource when it is insufficient for both or all of them; a *behavioural activity*, often, but not always, having negative consequences on RS (q.v.) of one or both interactants. In autecology broader definitions are confounding.

Competitive exclusion. The idea that two species having identical resource requirements cannot persist in the same area. The idea is confounded by immigration, mortality from enemies and environmental heterogeneity. It is largely supported by the type of thinking resulting in theoretical models rather than by the evidence of empirical field data.

Complexity theory. A general theory which states that at the base of complex systems lie a few simple rules.

Congregation. The act and result of mutual attraction by conspecifics.

Conservation biological control (**CBC**). The enhancement of the natural environment of a region to promote production, conservation and beautification (Section **13.2.4.7**).

Conspecific. Belonging to the same species.

Consummatory act. The final phase of a behavioural sequence.

Continuous variable. A variable that can have any value between two limits.

Convergent evolution. The independent evolution of structural and/or functional similarity in unrelated lineages. Thus, the process is not based upon overall genetic similarity. Q.v. **parallel evolution**.

Conversion efficiency (**CE**). The efficiency with which an insect converts its food into its own body mass. It varies from ~1% in some detritivores to ~50% in solitary bees.

Coriolis force. An apparent force due to the different velocity of points on the Earth's surface at different distances from the Equator.

Corm. The shortened and swollen stem base of a plant used as an organ of storage and often for asexual reproduction q.v. bulb.

Corpus allatum and corpus cardiacum. Two neurosecretory bodies associated with the insectan brain. Among other functions, they produce hormones that control flight fuels.

Correlation. A statistical relationship (+ or −) between two or more variables. Correlation does not imply causation.

Cosmopolitan. Worldwide. Hence, **cosmotropical**, throughout the tropics.

Cotyledon. The first leaves to sprout from the germinating seed. There may be one (Monocotyledons) or two (Dicotyledons) (Section **5.1**).

Counter shaded. Of animals that are dorsally dark and ventrally light, offsetting the effect of illumination from above. Thus they appear flat, for example some hawk moth caterpillars resemble leaves. (Section **5.2.1.03**(**b**)).

Crepuscular. Active at dawn and/or dusk.

Crop rotation. Growing a series of different crops on the same field. It avoids loss of soil fertility and the build-up of pests.

Cross resistance. The resistance to a given insecticide developed by an insect population that confers resistance to another insecticide yet unused.

Cryptic. Hiding.

Cryptic species. Species that are morphologically indistinguishable but in the field are reproductively isolated (q.v. sibling species). The term is particularly appropriate to taxa whose existence has recently been discerned within a well-studied former 'species'.

Cultivar. A cultivated variety of a crop or decorative plant.

Danger zone. In autecology a place or period in which inimical factors act with particular severity.

Day degrees (**D°**)**.** The number of degrees above the threshold for development times the number of days it occurs. For any population of an insect species a given number of day degrees is necessary to complete development.

De-coupled dynamics. Many population models of the interaction of victim and enemy assume that the density of the latter largely depends on that of the former. In de-coupled dynamics this is untrue.

Deduction. The generation of theory from incontrovertible axioms, which theory can be used to predict singular events.

Delivery system. The means by which an insecticide reaches the insect. It involves formulation and application.

Deme. A term often used in population genetics for a local group of freely interbreeding individuals.

Density dependence. In empirical data this means that there is a *significant* correlation between population density and either percentage mortality (density dependent mortality) or fertility (density-dependent natality). The term was originally coined by H.S. Smith (1935) and has also applied to dispersal and migration (Nicholson, 1933). Milne (1962) carefully distinguishes intraspecific competition (perfectly density dependent) from interspecific interactions including competition (imperfectly density dependent). Density dependence can be temporal or spatial (Richards, 1961) and its effect may be delayed. In models it means 'Some (nonconstant) functional relationship between the per capita rate of population change and population density, perhaps involving time lags' (Turchin, 2003).

Density-independent mortality. This occurs in empirical data when there is an *insignificant* correlation between population density and percentage mortality.

Dependent variable. In statistics a variable that is influenced by the magnitude of another variable.

Detritus. Fragmented, dead organic matter of animal or plant origin. We can conveniently recognize *phytodetritus* of plant origin, *zoodetritus* of animal origin and *coprodetritus* of faecal origin.

Developmental mortality. Mortality of juveniles (q.v.).

Diapause. A resting stage in the development of an insect that has enhanced resistance to an inimical physical condition, generally either cold or dryness.

Difference equations. These model population growth when the generations are discrete.

Differential equations. These model population growth when the generations are not discrete and reproduction is continuous.

Diploid. Having two sets of homologous chromosomes, normally one set from the father and one from the mother.

Diplodiploidy. Every male inherits one haploid genome from his father and another from his mother, both genomes having equal probability of being passed on via his sperm. Q.v. haplodiploidy.

Directional selection. Selection for an optimal phenotype resulting in a directional shift in gene frequencies coding for the character concerned. It leads to progressive adaptation in a changing environment.

Disassortative mating. The mating of like with unlike. Having some genetic basis it promotes greater variation among the offspring.

Discrete variable. A variable that can have only certain, discontinuous values.

Dispersal. As used in this book: non-appetitive movement within habitats (q.v.), often resulting in reduced population density (q.v. migration and redistribution).

Dispersion. The spatial distribution of organisms *at an instant in time*.

Disruptive selection. Selection for phenotypic extremes in a polymorphic population, hence accentuating discontinuity (q.v. stabilizing selection).

Dissipative structures. These are discrete regions of space that draw energy into themselves, increase in complexity, and finally senesce (McShea, 1998). An organism feeds on the surrounding entropy by taking in nutrients and expelling the waste that results.

Dosage response curve. The sigmoid curve resulting from assaying a series of dosages on large samples from a population. The dosages may be physical or chemical and vary from those causing very little to those causing almost total mortality. For factors such as lethal temperature, duration as well as intensity must be assayed.

Drag. In genetics, the differential replication of genes into the next generation at a rate <50% of the normal Mendelian rate of transmission.

Drive. The differential replication of genes into the next generation at a rate >50%. In one case genes increase in frequency at a given locus only. In the second case genes increase in frequency by colonizing other loci.

d_x factors. In a life table (q.v.) those factors killing the stated number of individuals within a given stage.

Eclosion. Hatching from the egg (from the French, *éclorer*, to hatch). Today the term is sometimes misused for emergence from the pupa, so promoting confusion.

Ecological efficiency. I propose this term to refer to the capability that individuals, and in sum the species to which they belong, possess to counteract environmental harshness. Harshness refers to both physico-chemical and biotic factors. Ecological efficiency also includes the ability to breed successfully under such conditions. Thus, the limits of moisture and temperature that some individuals can survive and reproduce are wider than those of others, while their ability to resist enemies, pathogens and resource competition also varies. Although some individuals may more efficiently resist adverse temperature and others may be better at thwarting enemies the term refers to the whole package.

Ecology. The study of individual organisms in relation to their physical and biotic environments. The definition derives from Haeckel, 1870.

Ecomones (= semiochemicals, q.v.). Compounds, usually borne in minute quantities in the air, that when detected may modify insect behaviour.

Edaphic. Pertaining to the soil.

e.g. (exempli gratia). For example.

Egg distribution. Referring to the fact that eggs may be deposited in one or several places, and in the latter case at different times. Egg distribution relates to semelparity or iteroparity (q.v.) and to the individual female's ability to seek resources, its ISC (q.v.).

EIL (= economic injury level). The level of crop pest attack at which economic loss begins. The economic threshold (ET) is the level at which controls should be applied to prevent an increasing pest population from reaching the EIL.

Emergence. Endopterygote adults *emerge* from the pupa.

Empirical. Based on direct observation.

Endemic. Native, and restricted to, a particular region (cf. exotic).

Endogenous factors. Generally biotic factors that have a reactive (two-way) relationship with the individuals under study.

Endophilic. Of insects living in human dwellings.

Endophytic. Of insects feeding from within plant tissue.

Endopterygote (= holometabolous) insects. Those having egg, larval, pupal and adult stages (q.v. exopterygote).

Endosperm. The nutritive tissue in the seeds of both angiosperms and gymnosperms.

Enemy. A generic term for predators, parasites, parasitoids and disease organisms. In enemy-free space individuals are relatively safe from these organisms (cf. refuge).

Entomophagous. Insect eating.

Entomophily. Pollination by insects.

Entomophthorales. A group of zygomycete fungi with several species that attack insects.

Environmental or ecosystem engineering. Physical changes to patches or habitats (q.v.) by dominant species, either plant or animal, that influence the ecology of a suite of other species. For example, the mud cells of some primary solitary wasps are used for nesting by secondary wasps and bees and their parasitoids. Here the action is non-trophic, but when a fungus forms a rot hole in a tree, a primary trophic event leads to patch creation for a group of organisms that are not involved in that event.

Environmental factors. Those factors external to the individual that influence its innate attributes (q.v.). They may be physico-chemical or biotic.

Environmental template. The entire ambit of migration of a given species. Also called the migratory arena by Drake *et al.* (1995).

Epidemiology. The scientific study of epidemic diseases.

Epistasis. In the genome a situation in which a gene not directly coding for a phenotypic trait nevertheless influences the activity of a gene that does so. It can also be described as a non-additive effect of an allele at a distinct locus. Q.v. additive genetic variance, non-additive genetic variance.

Epistemology. The theory of knowledge.

Estimate. Parameters (q.v.) are *estimated* by sample statistics.

Eukaryotes. Organisms compounded of cells with nuclei. They comprise all organisms except viruses, bacteria and Archaea.

Eusocial. Of groups (termites and Hymenoptera) showing fully integrated care of the juveniles. There are reproductive and non-reproductive workers.

Eutrophication. Water bodies act as nutrient traps. Over periods of time, appropriately measured in decades, their productivity builds up.

Evaporative rate. The rate of water loss from a given surface under the influence of temperature, humidity and wind speed.

Evapotranspiration. The total evaporative loss of water from an area from all sources, including transpiration from plants and evaporation from the soil and water bodies.

Evolutionary stable strategy (ESS). A behavioural strategy that is successful against other such strategies, even copies of itself.

Exogenous factors. Environmental factors that influence the focal species but are uninfluenced by it.

Exophilic. Of insects, particularly biting flies, living away from human dwellings.

Exophytic. Of insects feeding externally on plants.

Exopterygote (= hemimetabolous) insects. Those having only egg, nymphal and adult stages (q.v. endopterygote).

Exotic (opp. indigenous). Introduced from another country In popular parlance it has come to mean 'strangely beautiful and alluring', but we do not use that sense here.

Extant. Existing at a given time.

Extrapolation. Estimating a value(s) outside the range of the observed values.

Extrinsic theories of population. Those theories that emphasize factors extrinsic to the focal species (q.v.).

Exuvium. The cast cuticle of any developmental instar.

Facultative. Occasional.

FAO. The Food and Agricultural Organization of the United Nations.

Fecundity. The number of eggs laid by an individual female.

Fertility. The number of *fertile* eggs (= zygotes) laid by an individual female. Males can be fertile but not fecund.

Filariasis. Infestation with nematode worms belonging to the Filaroidea.

Fisher's Fork. The apportionment of metabolic resources to either survival or reproduction. The concept has been extended under the term 'trade-offs', see Table 6 in Danks (2007).

Fitness. The relative number of adult offspring left by different genotypes (cf. RS). The concept is confounded since not all offspring are themselves equally fit, so that the number of grandchildren may be a better measure (Hamilton, 1996). In addition, a distinction can be made between the fitness of individuals and the fitness of genes. The term is best linked to inclusive fitness (q.v.).

Focal species. In autecology (q.v.) the single species studied. I often term this 'our species'.

Forrest's maxim. The ability of insects to reach a resource quickly and in numbers, or be present in numbers early in the season (see Section **10.2.5.2** for further explanation).

Founder effect. A small group colonizing a new habitat (q.v. propagule) does not carry all the genes possessed by the species and thus may not be able to adapt to the new situation.

Frequency-dependent selection. Selection in which the frequency of a gene affects its fitness within a deme (q.v.).

Fruit. In angiosperms, a structure derived from the ovary after fertilization, which contains the seeds.

Fundamental theorem of natural selection. The rate of increase in fitness of any population at any time is equal to its genetic variance in fitness at that time (Fisher, 1930).

Fungi Imperfecti. A group of fungi known only from an asexual mycelium. Recent cytological evidence shows that most of them are Ascomycetes.

G × E Interactions. Interactions between genes and environment. There can be temporal and spatial aspects.

Games theory. A theory of optimum strategy where there is a contest between two or more players.

Gap phase. The seral (q.v.) changes that occur in mature forest after the fall of a large tree. Such phases are initiated by increased insolation.

Gaseous exchange. The conduction of oxygen to the tissues and carbon dioxide from them in connection with respiration.

Gene. The basic unit of inheritance comprising a specific sequence of nucleotides on a DNA chain. It occupies a specific **locus** on a chromosome, and codes for an RNA (q.v.), which usually in turn codes for a protein.

Gene flow. The passage of genes in time and space due to redistribution (q.v.) and reproduction.

Gene pool. All the extant genes (or DNA) in a given population.

Generalized (polyphagous) pests. Pests that attack a wide taxonomic range of crops.

Genes identical by descent. Genes in a population received by repeated segregation from a single gene in some common ancestor (Thompson, 1983).

Genetic conflict. There are two main sources of internal conflict in the individual: i) one results from different degrees of relatedness (q.v.) by different genetic elements; and ii) the differential replication of genes into the next generation (q.v. drive).

Genome. All the genes (or DNA) in a cell or organism that represents its heritable information.

Genotypic plasticity. The presence of considerable genetic variation in a population as a result of immigration, recombination and mutation.

Geographical isolation. The separation of potentially interbreeding populations by geological barriers. Such populations would be allopatric (q.v.).

Germ-line. Refers to that lineage of cells potentially leading to the gametes of the next generation. Opposite to **somatic** cells (q.v.).

Global population. The total number of individuals comprising a species. They may show various degrees of isolation from each other but are assumed to be potentially capable of interbreeding, as in the biological species concept.

Global regulation of numbers. The regulation of numbers comprising a global population.

Greenhouse gases. Atmospheric gases including water vapour, carbon monoxide, carbon dioxide and methane, which partially trap heat radiation from the Earth's surface, producing elevated temperatures. Without this effect the Earth would freeze.

Group selection. Those unusual cases of natural selection in which a group (population) of organisms is the focus. Better called inter-group selection.

Guild. A group of species that use the same type of environmental resource in a similar way.

Habitat. As used in this book: an area, often of the order of a hectare or more, usually containing several resource patches. Its structure often improves the environment of the focal species (q.v.) and may facilitate its dispersal. So, in crop ecology a field is a habitat.

Habitat heterogeneity. The concept that *natural* habitats have variable complexities. The main drivers of complexity are generally physical and edaphic factors that permit the biotic ones to evolve. In agricultural situations we partly suppress this natural variation.

Haematophagous. A general term literally 'blood eating', and referring to those arthropods that imbibe blood (q.v. ectoparasite, micropredator and myiasis).

Haemolymph. Insect blood pumped forward by the dorsal vessel but otherwise permeating the tissues. It does not function directly in gaseous exchange (q.v. tracheae).

Haldane's rule. J.B.S. Haldane (1922) noted that when only a single sex is sterile, whether male or female, that sex is the heterogametic (XY) one.

Handling time. The time taken by a predator to overcome and consume its prey before moving on to find the next one.

Haploid. Having only a single set of chromosomes, i.e. having only one of each type of chromosome.

Haplodiploidy. In this case every male develops from an unfertilized egg and has only a haploid genome inherited from his mother. Thus, he can transmit only this maternal genome. Females are all diploid.

Haplotype. The single species included in a genus at the time of its designation, so becoming the type species of the genus.

Harsh environment. An idea, originated by Darwin (1859) and extended by Andrewartha and Birch (1954), and by Greenslade (1983), that unfavourable physical conditions may dominate populations of animals living in such areas (q.v. kind environment).

Heliotaxis. A directed movement in relation to perception of the Sun's position.

Helminthic. Relating to parasitic worms. As far as transmission by insects is concerned the order Filaroidea is the most important.

Heritability. That part of the phenotypic variation that is genetically based. It is usually expressed as the ratio of the genetic to the phenotypic variance.

Hermaphrodite. An individual having the reproductive organs of both sexes.

Heterogametic sex (opp. homogametic). The sex producing two different gametes, i.e. X and Y sperm, and thus having different sex chromosomes.

Heterothermic. Of insects whose bodies remain near ambient temperature when resting but control their body temperature around a higher value when active.

Heterotrophic. Of organisms (animals) that eat a variety of organic foods.

Hibernaculum. A cocoon-like refuge made of silk and sometimes additional material in which a larva or occasionally larvae pass the winter.

Hibernation. Passing the winter in an inert phase (often diapause q.v.).

Histogram. When a continuous variate is chopped up into classes these may be graphed as columns whose heights are proportional to their frequency.

Hitch-hiking. The process by which a neutral allele increases in frequency because it is linked to a positively selected one.

Holistic. Related to an integrated whole, both physical and biotic.

Holobiont. The individual plus its symbionts considered as an evolutionary unit.

Horticulture. The culture of gardens.

Host. In this book, the *animal* victim of attack by a parasite, parasitoid or pathogen. This restricted definition avoids confusion when tritrophic interactions are being discussed.

Hydrological cycle. The global movement of water as ice, fluid or vapour between the sea, the land and the atmosphere. It involves evaporation, precipitation, advection (q.v.) and other flows, freezing and thawing.

Hydropyle. A group of cells in an insect egg capable of absorbing water against an osmotic gradient.

Hygrothermal. Referring to temperature and moisture conditions in combination.

Hypognathous. Of insect mouthparts (q.v.) in which the jaws work vertically; they are typical of herbivores and detritivores.

Idiobionts. Parasitoids (q.v.) that, if successful, quickly kill their host.

i.e. (id est). That is.

Ignorance in action. A common situation in modern societies in which actions, often affecting our environment, are taken without consulting those who are best able to advise.

Illuminance. The luminous flux per unit area falling perpendicularly on a surface.

Imago (pl. imagines, adj. imaginal). The adult insect.

Immune system. A physiological surveillance mechanism in individual vertebrates that specifically recognizes and selectively eliminates invading organisms.

Inbreeding. Mating among relatives. It can be quantified by *F*, Wright's inbreeding coefficient. It can also be the result of small population size. Q.v. assortative mating.

Inbreeding depression. The loss of genetic diversity due to mating among relatives.

Inclusive fitness. Total fitness of an individual compounded of fitness due to its own reproduction plus that of its relatives devalued by their genetic distance (Hamilton, 1964).

Individual searching capability (ISC; Section 9.3.4.1). As used in this book: the ability of an individual insect to seek and find distant, often multiple resources.

Indigenous. Native to a given region.

Induction. The gathering of empirical data that may be ordered to generate hypotheses.

Inflorescence. All the flowers on a single stem. There are several patterns.

Inimical factor. A factor that is unfavourable or hostile, such as bad weather or an enemy.

Innate attributes. In this book: properties of individuals including growth, survival, movement and reproduction (q.v. environmental factors). Such attributes are generally coded for by multiple alleles and collectively form life-history strategy.

Insolation. Incoming solar radiation.

Integrated pest management (IPM). The co-ordinated use of all appropriate methods of controlling a pest population.

Inter-Tropical Convergence Zone (ITCZ). The zone of maximum heating that moves between the Tropics of Cancer and Capricorn according to season, and where anabatic (q.v.) winds result in heavy rains.

Intrinsic theories of population. Those theories insisting that individual differences have an important and essential role in population regulation.

Isohyet. A contour line on a map drawn through areas of equal precipitation.

Juveniles. Insect stages that are not adult.

Juvenile hormone. An insect neurosecretion that prevents juveniles from becoming adults.

***K*-selection.** Selection for defensive and/or competitive ability, classically with low rates of redistribution. Q.v. *r*-selection.

Kairomone. An interspecific chemical messenger benefiting the recipient.

Karyotype. The entire set of chromosomes possessed by a cell, group or species. Thus the structural characteristics of the chromosome set and those individuals with an identical set of chromosomes.

Katabatic wind. A dense air mass flowing downward in response to gravity.

Kind environment. An environment having clement physical conditions thus permitting biotic interactions to have paramount importance on the animals living there (q.v. harsh environment).

Kinesis. The change in rate of the *random locomotory movement* of an individual as a result of a stimulus.

Kin selection. Selection on individuals mediated through genes identical by descent (q.v.) in relatives other than offspring.

Koinobiont. Of parasitoids (q.v.) that, even when successful, permit the host the chance to survive for an extended period.

Krogh's law. This law states that the rate of biological processes or events are directly related to temperature.

***K*-value analysis.** A popular means of analysing life table data using $\log_{10}$ values. But the method has increasingly been shown to be statistically flawed (see Royama, 1996).

Larva. The juvenile feeding stage in endopterygote insects.

LD_{50}. The intensity and duration of a physical or chemical mortality factor that kills 50% of an experimental population (LD_{95}, LD_{99}, etc.).

Leishmaniasis. Diseases of vertebrates caused by several species of the protistan genus *Leishmania* and including cutaneous, muco-cutaneous and visceral forms.

Life table. Tabulated mortality data from a sample of a population. They were gleaned from actuaries and are age-specific when based on the fate of a real cohort, or time specific when based on a time section through a continuously breeding population. Retrospective tables may be produced for a single or several accumulated generations from trace data (q.v.).

Life track. The path traversed by an individual in its entire lifetime.

Lignin. An amorphous macromolecule formed largely by random, non-enzymatic polymerization of modified monosaccharides and phenolic compounds. It forms the structural component of wood.

Logistic. A simplistic mathematical model of a population in which its growth is finally limited by the carrying capacity (q.v.).

l_x factors. In a life table (q.v.) the number of live individuals *entering* a given stage.

Malthusian parameter. The intrinsic rate of natural increase of a population with a given age distribution. It includes both births and deaths.

Markovian process. A process in which a present event is influenced by past events. A first-order process is influenced by only the last event, a second order process by the last two events, and so on. Such processes may be useful in analysing behavioural sequences.

Mate-specific recognition system. As an alternative theory to the Wallace effect (q.v.), the evolutionary development of such a system in an isolated population (= isolate) would promote speciation (Paterson, 1982).

Matrix. In spatial ecology, the space between habitats (q.v.). It is usually heterogeneous and provides various degrees of connectivity for a *low-level migrant* according to penetrability and distance.

Mean annual precipitation (MAP). The sum of water falling as rain, hail, snow and dew given in mm and averaged for many years. It is thus a component of climate.

Mechanical transmission. Of a pathogen transmitted by feeding that does not multiply in the vector.

Meiosis. The reduction division of diploid germ cells (q.v.) forming haploid gametes.

Menotaxis. A directed response of a mobile organism at a constant angle to the source of the stimulus.

Meta-analysis. The statistical synthesis of the results of separate studies.

Metabolism. The physiological and biochemical processes within the individual's body. They are divided into building processes (anabolism) and breaking down processes (catabolism).

Metapopulation. A series of local populations connected by migration (q.v.).

Micropredator. A small predatory insect that takes blood meals from its large prey without living on it (e.g. a mosquito) (Section **7.1.1.2**). Q.v. ectoparasite.

Migration. In this book: non-appetitive movement between habitats, often entailing considerable risk (q.v. redistribution and dispersal).

Milankovitch cycles (= orbital forcing variables). The long-term changes in the dynamic relationship between the Earth and the Sun, as follows: (i) *precession:* the Earth can be likened to a top slowly spinning and slightly wobbling about its axis (period 21,000 years); (ii) *axial tilt* (q.v.; period 41,000 years); and (iii) variation in the *eccentricity*, between limits of 147 and 151 million km, of the Earth's orbit around the Sun (period 100,000 years). They have significant effects on the long-term global climate.

Monocropping. Growing one crop continuously in the same field or area.

Monte Carlo method. A system of solving some statistical problems by the use of random sampling.

Morphological species. Species distinguished solely on morphological data.

Morpho-species. Species distinguished on morphological characters alone.

Mouthparts. A series of appendages on the insect head for manipulating and consuming the food. Mouthparts are either biting or sucking (Section **1.4.1**) although the latter is marginally a misnomer as pressure within the host or plant vessel may promote uptake.

mtDNA. Mitochondrial DNA.

Müllerian mimics. A group of harmful insect species that have evolved similar warning coloration, affording enhanced protection.

Multiple mating. Apart from increasing the genetic variation of the offspring, this often increases fecundity because of nutritive elements in the semen.

Multiplicative effect. Occurs in stored crops when the primary damage caused by an insect pest leads to extensive subsequent destruction by fungi and/or bacteria.

Multiplicative transmission. Of a pathogen that multiplies in the vector.

Murine. Pertaining to rats and mice (>1000 species. Rodentia; Muridae).

Mutualism. This occurs when two or more organisms live in close association for mutual advantage (= symbiosis q.v.).

Mycangia. Pockets, containing a fungal innoculum, that occur on the head, thorax or legs of bark beetles.

Mycelium. The mass of hyphae comprising the body of a fungus.

Mycorrhiza. A symbiosis (q.v.) between a fungus and the roots of plants.

Myiasis. The infestation of a living vertebrate animal, usually a bird or mammal, by dipterous larvae (see Section **7.1.1.3**).

Natality. Birth rate.

Natural control. The axiom that real populations remain between finite numerical limits.

Natural deception. Much information from animals is deceptive. This reduces or prevents exploitation by enemies. Cryptic coloration is a good example.

Natural enemy ravine. A phase in population growth predicted in the Southwood/Comins model in which enemies only temporally reduce the numbers of a victim population but with increasing density fail to do so.

Natural selection. The differential survivorship of organisms according to their hereditable inequalities under current environmental conditions. The main external creative agent of intraspecific and interspecific evolution.

Necron. Dead organisms or their parts (litter and cadavers) not yet sufficiently decomposed to form humus.

Nested clade analysis. An analysis of the gene tree of a presumptive species to investigate whether or not it represents a single species.

Niche. The role the focal species plays in the ecosystem. Other much wider and more complex definitions have been proposed, but since these may also include environmental space and assume the universality of competition they are inappropriate here.

Nicholsonian control. The theoretical mechanism in which populations are self-regulatory, there being a sufficient negative feedback on natality and survival at all densities.

Nitrogen fixation. The conversion of atmospheric nitrogen into useable nitrogenous compounds by micro-organisms that are often symbiotic.

Non-additive genetic variance. When alternative genes at a locus code for a particular trait their influence is not compounded. This is obviously true where a single gene at a locus is entirely dominant. A gene epistatic to another modifies its effect but is not additive. Q.v. additive genetic variance.

Nucleolus. That part of the cell nucleus in which rRNA is synthesiszd and ribosomal sub-units are assembled.

Number/density anomaly (NDA). Although numbers and densities within a restricted area such as a habitat are usually correlated, insect movement often confounds this relationship, so it is not precise (Taylor, 1984).

Numerical response. Of enemies that increase their numbers by reproduction within populations of their victims.

Nymph. The juvenile feeding stage in Exopterygota. There is no true pupa.

Obligate. Invariable.

Occam's Razor. Derived from William of Occam (d. circa 1350), one of the three 'Franciscan Schoolmen', this is the principle of testing the simplest hypothesis first.

Oligophagous. Eating a narrow taxonomic range of foods.

Ommatidium. The optical unit of the insectan compound eye. The visual acuity of these eyes depends on the number of such units, which in turn largely determines the angle between each one. In the best eyes this angle is <1°. Acuity also depends on the optical quality of each unit (Land, 1997).

Onchocerciasis. Infestation of the human skin including the conjunctiva of the eye by the filarial worm *Onchocerca volvulus*, which is transmitted as an anthroponosis (q.v.) in sub-Saharan Africa and parts of the Neotropics by several species of *Simulium*. The resulting disease, river blindness, results from an immune reaction in the eye to the α-proteobacterium *Wolbachia* contained in the worms.

Oogenesis-flight syndrome. A term referring to the fact that redistribution and reproduction are usually separate phases in the life of an individual adult insect.

Optimal (opp. pessimal). Most favourable.

Optimal foraging. The hypothesis that natural selection (q.v.) favours individuals that maximize energy gain relative to energy expenditure during unit foraging time.

Optomotor reaction. The ability of some flying insects to assess their ground speed by the apparent motion of objects passing beneath them.

Organic and inorganic localization. The concentration of living or dead material in the environment. It occurs either by redistribution, or by the growth of an organism(s). In the first case, both physical and biotic forces move such material non-randomly. The concept is part of a wider principle of order arising from disorder due to Ilya Prigogine (1980). Of course, order also arises from order, as in animal and plant reproduction.

Ortet. The original individual from which a clone was derived.

Outbreeding. Effectively disassociative mating (q.v.), often from distant populations.

Over-dominance. Superior phenotypic expression of the heterozygote at a locus over both homozygotes.

Over-sowing. To offset mortality, sowing more seed than can develop into mature plants.

Pandemic. An epidemic that is synchronous and widespread.

Panmixia. Population-wide random mating.

Paradigm. Showing side by side. (Fowler's definition). An exemplary situation. In science this has come to describe a *way of seeing*, or a *shared common view*, something that is *larger and more general than a hypothesis*, or *an intellectual framework within which investigation proceeds*.

Parallel evolution. Similar evolutionary changes appearing in different lineages, q.v. convergent evolution.

Parameters. The true means, variances, etc. relating to the entire population or 'universe' (q.v.). They may be estimated by statistics (q.v.) derived from representative samples.

Parametric. Of statistical distributions that are potentially continuous (e.g. the wing lengths of a sample of a single locust species).

Parapatric. Of populations whose geographical distributions are contiguous but do not overlap. Gene flow between them is possible but limited (q.v. Allopatric, Sympatric).

Parasitaemia. The intensity (= population density) of parasites within the blood.

Parasite. An animal smaller than its host (q.v.) and living on it (ectoparasite (Section **7.1.1.1**)) or in it (endoparasite) and at its expense. Parasites generally do not kill their hosts although they weaken them and hence may predispose them to enhanced mortality from other inimical factors.

Parasitoid. Normally entomophagous, *endopterygote* insects that are 'parasite like'. The name was originally promoted in the belief that parasitoids, unlike parasites, generally kill their hosts. Accumulating evidence shows that host insects often recover from such attacks (Section **8.2.2.5**). But since the association is essentially an 'arms race' (q.v.) it cannot evolve into mutual accommodation, as can the true parasite/host system.

Parental investment. The investment of time and energy by either sex to promote the survival and reproductive success of their existing offspring at the expense of such investment in future offspring.

Parity. In semelparous species individuals reproduce once only (like salmon). In iteroparous species individuals may reproduce several times (like us).

Parous rate. The proportion of adult female vectors that have laid eggs. This is normally estimated by dissection and inspecting the condition of the ovaries.

Parthenogenesis. Reproduction by unfertilized females; thus embryogenesis from an unfertilized egg.

Pathogen. The source of a pathological condition, often a micro-organism.

Pedology. The scientific study of soils.

Peridomestic. Around human dwellings.

Peruvian bark. The bark of the tree *Cinchona pubescens*, originally used by the Andean Amerindians to suppress fevers and later found to be the source of quinine.

Pharate stages. H.E. Hinton (1946) proposed this term for a fully formed instar enclosed in the cuticle of the preceding stage.

Pharotaxis. Navigation by means of landmarks.

Phenology. The temporal relations of the life history.

Phenotype. The product of interaction between the genotype and its total environment (both internal and external) expressed in the individual, and upon which natural selection acts. One cannot investigate a genotype unless 'the phenotypic facts of translation' (Watt, 2000) from the base pair code are known.

Phenotypic plasticity. The capacity for considerable variation in the phenotype resulting from environmental influences during development.

Pheromone. An intraspecific, usually complex, chemical messenger. When they are sensed by a heterospecific they may act as kairomones (q.v.). See also semiochemicals.

Phloem. Vascular tissue that conducts the bulk of plant metabolites.

Phoresy. The transport of one individual by another, e.g. the fly *Braula* on bees.

Photoperiod. The period of daylight relative to the period of darkness.

Phreatic. Pertaining to ground water.

Phyletic. Relating to a line of evolutionary descent.

Phytotelmata. Plants, such as bromeliads, that hold free water for some time.

Phytotoxic. Toxic to plants.

Planidium. The flattened, mobile, first larval instar found in a few families of parasitic wasps, such as the Platygasteridae and the Eucharitidae.

Plant association. A general term, irrespective of spatial scale, for plants living together.

Plant communities. The primary divisions of a biome (q.v.) relative to plants.

Pleiotropic. The frequent situation (Caspari, 1952) in which a single gene affects more than one phenotypic character, apparently independently. Wright's view (1982) is that this results from the interaction of genic products.

Poikilothermic (opp. homoiothermic). Animals that do not regulate their own body temperature metabolically: cold blooded.

Poisson distribution. Random distribution (q.v.).

Polyembryony. Reproduction in which an egg develops into several, often numerous, progeny.

Polygenic. Of phenotypic traits controlled by the co-ordinated action of a group of genes.

Polymorphism. The occurrence together of two or more *discontinuous* forms of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation.

Polyphagous. Eating a wide taxonomic range of foods. However, some foods are preferred over others, and these will commonly confer greater RS (q.v.).

Polyphenism. The occurrence together of two or more distinct phenotypes induced by extrinsic factors in individuals of the same genotype.

Population. Conspecific individuals sharing the same gene pool (q.v.). Given this, there are broad and narrow definitions: i) Turchin's (2003) broad definition: a group of conspecific individuals living within a defined area large enough to enclose all migration and dispersal; and ii) my own narrow definition: a group of conspecific insects occupying a habitat (q.v.).

Population cycles. The fluctuation of population numbers often has an apparently regular fluctuation. The regularity of the cycles, however, should be proved to be significantly different from random.

Population limitation. The mechanism resulting in zero or negative population growth as the carrying capacity is approached. This may result from diverse density-dependent or imperfectly density-dependent processes (q.v.) on natality, survival and emigration.

Population stability. The observed relative constancy of population size through time, showing no trend of increase or decrease and fluctuations that are much less than expected on the basis of a potentially high rate of population increase.

Population unit. The smallest unit of potentially interacting, conspecific individuals. They occupy a patch (q.v.).

Postulate. A probable situation: e.g. populations are regulated about a mean value; q.v. axiom.

Prairie. A grassland biome (q.v.) in which tall grasses predominate.

Predictable. Of events that may be forecast with a probability at or close to unity.

Pre-reproductive mortality. Of adults, particularly females, dying before reproduction. Often its magnitude has been much underestimated.

Primary food plant. Polyphagous insects are usually found more frequently on some plant species than on others. These primary foods often confer higher reproductive success (q.v.) than others do.

Primary production. The synthesis by primary producers (e.g. by plants) of often complex organic compounds from simple inorganic substrates.

Probability. The chance that a given event will occur on a scale of zero (impossibility) to unity (inevitability).

Prognathous. Of insect mouthparts (q.v.) in which the jaws work horizontally. They are typical of predators.

Propagule. A vegetative structure that on becoming detached from its parent may grow into a separate plant. The term is often used more generally to describe a local group of invading organisms.

Proteome. The entire complement of proteins expressed by a genome, cell, tissue, or organism at a given time under defined conditions (Libersat *et al.*, 2009).

Proximate factor. The immediate cause of an event (cf. *ultimate factor*).

Pupa. In endopterygote insects this is the *stage of change* between the larva and the adult.

Qualitative. Descriptive and non-numerical.

Quantitative. Of properties that can be put on a numerical scale.

Quiescent. A general term for a temporary resting stage, not necessarily diapause (q.v.).

q.v. (quod vide). Which see.

***r*-selection.** Selection for high reproductive rate, and usually high dispersal. Q.v. *K*-selection, adversity selection.

Rain shadow area. That region on the leeward of high ground that receives reduced rainfall.

Random. Without recognizable pattern; haphazard; stochastic. In time series uninfluenced by past events.

Random distribution. The statistical distribution that results when spatial or temporal events occur without relation to each other.

Random genetic drift (RGD). Through the generations chance itself, due to sampling errors, gradually changes the frequency of genes in a population. It takes place in the absence of selection and migration but its effect is inversely related to population size, and it is thus important only in small populations. RGD was originally suggested by Hagedoorn (1921) see Fisher (1922).

Random sample. A sample in which every member of a population has an equal and independent chance of being included.

Ranked data. Numerical data ordered according to magnitude.

rDNA. Ribosomal DNA; the genes encoding rRNA.

Real mortality. In a life table (q.v.) the number of individuals dying within a given stage as a proportion of the number of eggs laid.

Redistribution. The generic term for dispersal and migration (q.v.).

Refractory or latent period. That period in which a pathogen is multiplying within a vector but is not capable of being transmitted.

Refuge. A micro-environment or period of time in which the individual is at relatively low risk of death.

Refuge habitat. A habitat in which the adverse season is passed but in which reproduction does not occur.

Regionally rich. Of local floras or faunas containing an unusually high number of species.

Regulation. Refers to the fact that a population remains between finite limits. Milne refers to this process as natural control (q.v.).

Reinforcement. The process in which two populations, having evolved some post-zygotic isolation in allopatry, undergo selection for enhanced sexual isolation when later they become sympatric. Although the existence of the process has been equivocal, strong supportive evidence has been obtained for *Drosophila* species (Coyne and Orr. 1998) and for several other taxa (Servedio and Noor, 2003).

Relative humidity. The percentage of water vapour present in the air relative to that of saturation at the same temperature.

Reproductive success (RS). Measured as the number of offspring surviving to reproductive age (cf. fitness).

Rescue effect. Small or peripheral populations, including those comprising metapopulations, would frequently go extinct but for the rescue effect of immigration.

Reservoir host. A host that carries a pathogen with little detriment to itself and which serves as a reservoir of infection for alternative hosts.

Reservoir food plant. An alternative food plant, often a wild relative of a crop species, that maintains a pest herbivore in addition to, or in the absence of, that crop.

Resource patch (patch). As used in this book: the smallest association of resources allowing the reproduction of an insect species.

Rhizome. A horizontal underground stem.

Rickettsiae. Diverse Gram-negative bacteria that live only within the cells of both arthropods and mammals. Among other diseases they cause various forms of typhus.

Risk spreading. An idea promoted by P.J. den Boer that in an unpredictable world the generation of variation has selective advantage.

Sahel. A band of semi-desert to the south of the Sahara.

Salivary cocktail. The saliva of micropredators (q.v.), containing a variety of vaso-dilatory, anti-coagulant and possibly pain-inhibiting substances.

Saproxylic. Of insects that digest woody tissue with the aid of symbiotic (q.v.) micro-organisms.

Scatter diagram. A plot on two axes of paired data points, e.g. the height and weight of a series of individuals. Similar three-dimensional plots naturally require three data points.

Seed. A reproductive structure in higher plants developed from the fertilized ovule. It comprises an embryo, a food store (endosperm q.v.) and a protective coat.

Selection. Non-random differential reproduction of different genotypes in a population (q.v. balancing selection, directional selection, disruptive selection, stabilizing selection).

Selective mosaic. When a population, or indeed the progeny deposited by a single female, inhabits several patches or adjacent habitats, it will be subject to a diversity of selective forces relative to the area it occupies.

Self-sterility gene. A gene that prevents self-fertilization in monoecious plants by limiting the growth of the pollen tube.

Selva. Tropical rain forest.

Semiochemicals (= ecomones). Compounds, usually borne in minute quantities in the air, that when detected may modify insect behaviour. They may be intraspecific (pheromones) or interspecific (allelochemicals). For the latter, they may be mutually beneficial (synomones), neutral for the producer and beneficial to the receiver (allomones), or harmful to the producer and beneficial to the receiver (kairomones).

Sere (adj. seral). One phase in a series of progressive floristic changes in a plant community (q.v.).

Serotinal. Pertaining to late summer.

Shorter Oxford English Dictionary (SOED). The standard work in English in two volumes.

Sibling species. Related species that cannot be separated morphologically by normal micro-scopical means, but are mutually sterile: i.e. good biological species (q.v. cryptic species).

Sink population. A population in which deaths exceed births and is thus maintained by immigration. In an absolute sink although resources are available no viable adult offspring can be produced.

Sociobiology. The scientific, biological study of societies.

Somatic. Refers to the body of an organism, particularly those cells not in the germ-line (q.v.).

Spanandry (opp. spanogyny). The occurrence of few males in a population.

Specialized (oligophagous) pests. Those attacking a narrow taxonomic range of crops.

Speciation. The process, from whatever causes, by which new species are formed from a pre-existing one(s). The development of *isolating mechanisms* is held to be the common cause of species formation, but the development of *mate-specific recognition* (q.v.) may well be important. Speciation may be *allopatric* when species diverge from a common stock in spatial isolation, *parapatric* when two such stocks are contiguous, and *sympatric* if speciation occurs within a population. Also, infectious speciation may result when *Wolbachia* causes hybrid inviability (Coyne, 1992). (q.v. barriers to interspecific mating and biological species).

Spermatophore. A lipoprotein body transferred during mating from male to female and enhancing fecundity.

Sperm competition. The ultimate level of competition for mates, that between the sperm of different males.

Spirochaeta. A class of bacterium with a spiral body form (e.g. *Borrelia* and *Treponema*).

Sporozoite rate. The proportion of a sample of female *Anopheles* mosquitoes carrying infective sporozoites of *Plasmodium* in their salivary glands.

Stabilizing selection. Selection towards a mean value for a trait. Q.v. disruptive selection.

Steppe. A semi-arid, Eurasian grassland biome (q.v.) in which short grasses predominate.

Sterile male technique (SMT). The release of large numbers of irradiated, sterile males into a pest population to mate with wild females. An increasing proportion of infertile eggs is thus produced, driving the pest population to extinction.

Super gene. A tightly linked group of genes normally transmitted together.

Superparasitism. In entomology, this occurs when more than one parasitoid leaves progeny in a single host, or when a single female leaves more than the normal complement.

Symbiosis. In this book: the same as mutualism (q.v). Some workers use the term without specifying mutual benefit.

Sympatric. Used of individuals, populations or species living in the same geographical area.

Synecology (= biocoenotics). The branch of ecology that examines communities.

Systemic insecticide. One that is translocated within the plant's vascular system.

Taiga. Northern coniferous forest (pronounced 'tiger').

Tap root. In dicotyledons, the main root derived from the radicle of the germinating seed.

Tautology. The unnecessary repetition of a word or statement.

Taxis (pl. taxes). Locomotion directed with respect to a given stimulus.

Taxon (pl. taxa). Any unit of biological classification (e.g. species, genus, family, class).

Taxonomy. The branch of biology that deals with the classification of living or fossil forms.

Taylor's power law. This states that the aggregation of a population throughout its range of densities is described by $s^2 = am^b$, where s^2 is the variance, a depends on the size of the sampling unit, m is the mean and b is an index of aggregation (and a fractional power). It is very generally valid.

Teneral. Of an instar before its cuticle has hardened.

Tetrapods. Those animals having, or originally having, four legs, namely all terrestrial vertebrates.

Thelytoky. The production of only female eggs by unmated mothers. There are no males.

Therophyte. Annual plants that survive the unfavourable period as seeds.

Tillage. A general term for the physical manipulation of the soil. It includes ploughing, harrowing and discing. In conservation tillage, which is practised on soils at risk of erosion, crops are grown in relatively untilled soil with surface residues from the previous crop. Minimum tillage ('mintil') is similarly superficial and practised to save fuel costs.

Token stimulus. A stimulus that acts for something else.

Top-down effects. Factors acting from higher up in the food chain. Q.v. bottom-up effects.

Trace data. Insects often leave traces of their activities. Sometimes the traces are so comprehensive that they can be used to form a life table (q.v.).

Tracheae. Spirally strengthened pipes running though the insect's body, which effect gaseous exchange (q.v.). The system may include air sacs that assist gaseous exchange.

Trait. Normally, an observable characteristic of individuals determined by the unordered pair of types of two homologous genes. Polygenic traits are coded for by several alleles q.v.

Transcriptome. The transcribed set of messenger RNA molecules present in the cytoplasm at the time the sample is taken (Stearns and Magwene, 2003).

Transgenic. Of organisms, often crop plants, which have received genetic material from another species by genetic engineering. Hence, transgenic insecticidal cultivars (TICs), for those expressing toxins against insects.

Tritrophic. Referring to three consecutive, interactive levels in the food chain.

Triungulin. The minute, mobile first instar larvae of several parasitoid groups, including some Tachinidae, the Meloidae and the Strepsiptera.

Truly selfish genes. These spread in a population in spite of the fact that they inflict a cost to the organism itself, that is, on most of the rest of the genotype in which they reside (Trivers, 2008).

Trypanosomiasis. Diseases of tetrapods caused by the protistan genus *Trypanosoma* and including sleeping sickness, Chagas' disease and Surra.

Tuber. A storage organ found in dicotyledons that is derived from the root (root tuber) or stem (stem tuber).

Ultimate factor. The final cause of an event or situation. For example, the proportion of humus in the soil *proximally* depends on the amount of vegetation present, which in turn *ultimately* depends on the amount of rainfall. The concept was used by Thomas Aquinas as a proof of God's existence, namely He is the ultimate cause of the universe.

Universe. In statistics, the entire population being sampled.

Vagile. Freely mobile and wandering.

Variation. Particularly in genetics, the amount of existing difference, c.f. variability, the potential to vary.

Vector. An arthropod or other invertebrate that transmits a pathogenic organism. In this book we also use the term as a verb. The word is used differently in mathematics and in genetic engineering.

Vertical transmission. Of a pathogen, usually a virus, that is directly transmitted between generations of the vector, often in the egg. In triatomine bugs trypanosomes may pass among the population as a result of cannibalism.

Victim. An individual subject to attack by an enemy (q.v.).

Vittae. Lengthwise stripes on an insect's integument.

Voltinism. Refers to the number of generations per year (univoltine, bivoltine, etc.).

Wallace effect. The final process in the formation of two species from an ancestral one due to the low fitness of hybrids. This process is referred to as outbreeding depression (cf. in-breeding depression). That the hybrids 'compete' (q.v.) with either parent stocks is an unnecessary assumption: they need only have death rates in access of birth rates.

WHO. The World Health Organization of the United Nations.

Williams' effect. As used in this book: when the duration of development is extended for any reason, mortality factors acting at a constant rate will kill a greater number of the animals concerned (after G.C. Williams, 1966).

World War One (1914–1918) and World War Two (1939–1945) (WWI and WWII). Although there was effectively global involvement, these wars were particularly disruptive to Europe, Australia, Russia and Japan. They caused human destruction measured in tens of millions and while they promoted developments in technology they were stagnant periods for biology.

Xerophyte. A plant found in and adapted for dry locations.

Xylem. That part of the plant's vascular system that transports mainly water.

Yield compensation. A situation in which, although a pest destroys a part of the crop this does not effect the final yield, either because new plants spring in to replace ones destroyed (grain and cane), or because the plant produces more fruits than it can mature, and naturally excises the surplus (cotton, top fruits). In a few crops, such as soya beans, yield is actually improved by the removal of leaves.

Zoonosis. The transmission of pathogens that, apart from the vector, involve tetrapods other than man.

Zoophilic. Of micropredators (q.v.) that bite tetrapods other than man.

Zygote. A diploid cell formed by the fusion of a male and a female gamete.

References

Abate, Y., Van Huis, A. *et al.* (2000) Pest management strategies in traditional agriculture: an African perspective. *Annual Review of Entomology* 45, 631–659.

Abbott, C.H. (1951) A quantitative study of the migration of the Painted Lady butterfly, *Vanessa cardui* L. *Ecology* 32, 155–171.

Abe, J., Kamimura, Y. *et al.* (2009) Extremely female-biased primary sex-ratio and precisely constant male production in a parasitoid wasp *Melittobia*. *Animal Behaviour* 78, 515–523.

Abe, J., Innocent, T.M. *et al.* (2010) Virginity and clutch size behaviour of a parasitoid wasp where mothers mate their sons. *Behavioral Ecology* 21, 730–738.

Abe, T., Bignell, D.E. (2000) *Termites: Evolution, Sociality, Symbiosis*. Dordrecht, The Netherlands: Kluwer.

Abrams, P.A. (2000) The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* 31, 79–105.

Abrams, P.A. and Ginzburg, L.R. (2000) The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution* 15, 337–341.

Abrams, P.A. and Matsuda, H. (1996) Positive indirect effects between prey species that share predators. *Ecology* 77, 610–616.

Ackerman, J.D. (1983) Specificity and mutual dependence of the orchid-euglossine bee interaction. *Biological Journal of the Linnean Society* 20, 301–314.

Ackerman, J.D. and Montalvo, A.M. (1985) Longevity of euglossine bees. *Biotropica* 17, 79–81.

Adams, C.D. (1972) *Flowering Plants of Jamaica*. Mona, Jamaica: University of the West Indies Press.

Addicott, J.F. (1978) The population dynamics of aphids on fire weed: a comparison of local populations and metapopulations. *Canadian Journal of Zoology* 56, 2554–2564.

Addo-Bediako, A., Chown, S.L. *et al.* (2002) Metabolic cold adaptation in insects: a large-scale perspective. *Functional Ecology* 16, 332–338.

Ager, D. (1993) *The New Catastrophism. The Importance of the Rare Event in Geological History*. Cambridge, UK: Cambridge University Press.

Agrios, G.N. (2005) *Plant Pathology*. London, UK: Elsevier/Academic Press.

Alam, M.M., Bennett, F.D. *et al.* (1971) Biological control of *Diatraea saccharalis* (F.) in Barbados by *Apanteles flavipes* Cam. and *Lixophaga diatraeae* T.T. *Entomophaga* 16, 151–158.

Albuquerque, G.S., Tauber, M.J. *et al.* (1997) Life-history adaptations and reproductive costs associated with specialisation in predacious insects. *Journal of Animal Ecology* 66, 307–317.

Al Deeb, M.A., Wilde, G.E. *et al.* (2001) No effect of *Bacillus thuringiensis* corn and *Bacillus thuringiensis* on the predator *Orius insidiosus* (Hemiptera : Anthocoridae). *Environmental Entomology* 30, 625–629.

Alexander, R.D. (1964) The evolution of mating behaviour in arthropods. *Royal Entomological Society of London, Symposium* 2, 78–95.

Alford, D.V. (1975) *Bumblebees*. London, UK: Davis-Poynter.

Alford, D.V. (2007) *Pests of Fruit Crops*. London, UK: Manson Publishing.

Allan, S.A., Day, J.F. *et al.* (1987) Visual ecology of biting flies. *Annual Review of Entomology* 32, 297–316.

Allee, W.C. (1932) *Animal Aggregations: A Study in General Sociology*. Chicago, Illinois, USA: University of Chicago Press.

Allee, W.C., Emerson, A.E. *et al.* (1949) *Principles of Animal Ecology*. Philadelphia, Pennsylvania, USA: Saunders.

Allen, J.A. (1988) Reflexive selection is apostatic selection. *Oikos* 51, 251–253.

Allison, J.D., Borden, J.H. *et al.* (2004) A review of the chemical ecology of the Cerambycidae. (Coleoptera). *Chemoecology* 14, 123–150.

Alphey, L., Beard, C.B. *et al.* (2002) Malaria control with genetically manipulated insect vectors. *Science* 298, 119–121.

Alstad, D.N and Andow, D.A. (1995) Managing the coevolution of insect resistance to transgenic plants. *Science* 268, 1394–1396.

Altenkirch, V.W. (1991) Zyklische Fluktuation beim Kleinen Frostspanner (*Operophtera brumata* L.) [Cyclic fluctuation of winter moth (*Operophtera brumata* L.)] *Allgemeine Forst und Jagdzeitung* 162, 2–7.

Altieri, M.A. (1990) The agro-ecology of temperate cereal fields: entomological implications. In: Firbank, L.G., Carter, N. *et al.* (eds) *The Ecology of Temperate Cereal Fields*. London, UK: Blackwell, pp. 259–272.

Altner, H., Routil, C.H. *et al.* (1981) The structure of bimodal chemo-, thermo-, and hygroreceptive sensilla on the antenna of *Locusta migratoria*. *Cell and Tissue Research* 215, 289–308.

Alto, B.W., Lounibos, L.P. *et al.* (2008) Larval competition alters susceptibility of adult *Aedes* mosquitoes to dengue infection. *Proceedings of the Royal Society B* 275, 463–471.

Aluja, M. (1994) Bionomics and management of *Anastrepha*. *Annual Review of Entomology* 39, 155–178.

Aluja, M. (1996) Future trends in fruit fly management. In: Aluja, M. and Liedo, P. (eds) *Fruit Flies Biology and Management*. New York, New York, USA: Springer, pp. 309–320.

Aluja, M. and Mangan, R.L. (2008) Fruit fly (Diptera: Tephritidae) host status determination: critical conceptual, methodological, and regulatory considerations. *Annual Review of Entomology* 53, 473–502.

Alves, F.P., Gil, L.H.S. *et al.* (2005) Asymptomatic carriers of *Plasmodium* spp. as infection source for malaria vector mosquitoes in the Brazilian Amazon. *Journal of Medical Entomology* 42, 777–779.

Alves, A.P., Spencer, T.A. *et al.*(2006) Inheritance of resistance to the Cry1Ab *Bacillus thuringiensis* toxin in *Ostrinia nubilalis* (Lepidoptera: Crambidae). *Journal of Economic Entomology* 99, 494–501.

Ames, C., Turner, B. *et al.* (2006) The use of mitochondrial cytochrome oxidase 1 gene (CO1) to differentiate two UK blow fly species – *Calliphora vicina* and *Calliphora vomitoria*. *Forensic Science International* 164, 179–182.

Anderson, C.R., Spence, L. *et al.* (1961) Oropouche virus: a new human disease agent from Trinidad, West Indies. *American Journal of Tropical Medicine and Hygiene* 10, 574–578.

Anderson, J.F. (1968) Influence of photoperiod and temperature on the induction of diapause in *Aedes atropalpus* (Diptera: Culicidae). *Entomologia Experimentalis et Applicata* 11, 321–330.

Anderson. R.M. and May. R.M. (1992) *Infectious Diseases of Humans: Dynamics and Control*. Oxford, UK: Oxford University Press.

Andersson, J., Borg-Karlson, A-K. *et al.* (2003) Anti-aphrodisiacs in pierid butterflies: a theme with variation. *Journal of Chemical Ecology* 29, 1489–1499.

Andersson, M. (1994) *Sexual Selection*. Princeton, New Jersey, USA: Princeton University Press.

Andersson, P. and Hambäck, P.A. (2012) What shapes local density? The importance of migration rates and local growth for density-patch size relationships in two *Cionus* weevils. *Ecological Entomology* 37, 90–98.

Andreassen, L.D., Kuhlmann, U. *et al.* (2010) Spring emergence of Canadian *Delia radicum* and synchronization with its natural enemy, *Aleochara bilineata*. *The Canadian Entomologist* 142, 232–249.

Andrewartha, H.G. (1970) *Introduction to the Study of Animal Populations*, 2nd edn. London, UK: Methuen.

Andrewartha, H.G. and Birch, L.C. (1954) *The Distribution and Abundance of Animals*. Chicago, Illinois, USA: The University of Chicago Press.

Andrewartha, H.G. and Birch, L.C (1984) *The Ecological Web*. Chicago, Illinois, USA: The University of Chicago Press.

Andrewartha, H.G. and Browning, T.O. (1961) An analysis of the idea of “resources” in animal ecology. *Journal of Theoretical Biology* 1, 83–97.

Anitha, V., Wightman, J. *et al.* (2005) Management of white grubs (Coleoptera: Scarabaeidae) on groundnuts in southern India. *International Journal of Pest Management* 51, 315–322.

Anon. (1980) *The New Shorter Oxford English Dictionary*. Oxford, UK: Clarendon Press.

Anon. (1982) *The Locust and Grasshopper Agricultural Manual*. London, UK: Centre for Overseas Pest Research.

Anon. (1993) *The New Shorter Oxford English Dictionary*. Oxford, UK: Clarendon Press.

Anon. (1997) *The Times Atlas of the World*, Concise edn. London, UK: Times Books.

Anton, C., Zeisset, I. *et al.* (2007) Population structure of a large blue butterfly and its specialist parasitoid in a fragmented landscape. *Molecular Ecology* 16, 3828–3838.

Antonovics, J. (1987) The evolutionary dys-synthesis: which bottles for which wine? *The American Naturalist* 129, 321–331.

Antonovics, J. and van Tienderen, P.H. (1991) Ontoecogeno phyloconstraints? The chaos of constraint terminology. *Trends in Ecology and Evolution* 6, 166–168.

Aoki, S. (1977) A new species of *Colophina* (Homoptera: Aphidoidea) with soldiers. *Kontyu* 45, 333–337.

Applegate, R.D. (1999) Diversity and natural history observation in ecology. *Oikos* 87, 587–588.

Archetti, M., Döring, T.F. *et al.* (2008) Unravelling the evolution of autumn colours: an interdisciplinary approach. *Trends in Ecology and Evolution* 24, 166–173.

Arditi, R. and Ginsburg, L.R. (1989) Coupling in predator-prey dynamics: ratio dependence. *Journal of Theoretical Biology* 139, 311–326.

Armstrong, R.A. and MacGehee, R. (1980) Competitive exclusion. *The American Naturalist* 115, 151–170.

Armstrong, T. (1958) Life history and ecology of the plum curculio, *Conotrachelus nenuphar* (Hbst.) (Coleoptera: Curculionidae). *The Canadian Entomologist* 90, 8–17.

Arnett, R.H. (1993 originally published in 1985) American Insects. *A Handbook of the Insects of America North of Mexico*. Gainesville, Florida, USA: Sandhill Crane Press.

Arnold, S.J (1992) Constraints on phenotypic evolution. *The American Naturalist* 140, S85–S107.

Arnqvist, G. and Nilsson, T. (2000) The evolution of polyandry: multiple mating and female fitness in insects. *Animal Behaviour* 60, 145–164.

Arthur, A.P. (1966) Associative learning in *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae). *The Canadian Entomologist* 98, 213–223.

Arthurs, S., Heinz, K.M. *et al.* (2004) An analysis of using entomopathogenic nematodes against above-ground pests. *Bulletin of Entomological Research* 94, 297–306.

Ascherson, N. (1995) *Black Sea*. London, UK: Jonathan Cape.

Asher, J., Warren, M. *et al.* (2001) *The Millennium Atlas of Butterflies in Britain and Ireland*. Oxford, UK: Oxford University Press.

Ashraf, M. and Berryman, A.A. (1970) Biology of *Sulphurethylenchus elongatus* (Nematoda: Sphaerulariidae), and its effects on its host, *Scolytus ventralis* (Coleoptera: Scolytidae). *The Canadian Entomologist* 102, 197–213.

Asiimwe, P., Ecaat, J.S. *et al.* (2006) Life-table analysis of mortality factors affecting populations of *Bemisia tabaci* on cassava in Uganda. *Entomologia Experimentalis et Applicata* 122, 37–44.

Askew, R.R. (1971) *Parasitic Insects*. London, UK: Heinemann.

Askew, R.R. and Shaw, M.R. (1974) An account of the Chalcidoidea (Hymenoptera) parasitising leaf-mining insects of deciduous trees in Britain. *Biological Journal of the Linnean Society* 6, 289–335.

Askew, R.R. and Shaw, M.R. (1986) Parasitoid communities: their size, structure and development. In: Waage, J.K. and Greathead, D.J. (eds) *Insect Parasitoids*. London, UK: Academic Press, pp. 225–264.

Asplen, M.K., Bano, N. *et al.* (2014) Specialisation of bacterial endosymbionts that protect aphids from parasitoids. *Ecological Entomology* 39, 736–739.

Assefa, Y., Mitchell, A. *et al.* (2008) Establishment of *Cotesia flavipes* (Hymenoptera: Braconidae) on sugarcane fields of Ethiopia and origin of founding population. *Journal of Economic Entomology* 101, 686–691.

Atkins, M.D. and Farris, S.H. (1962) A contribution to the knowledge of flight muscle changes in the Scolytidae (Coleoptera). *The Canadian Entomologist* 94, 25–32.

Atkinson, W.D. (1985) Coexistence of Australian rainforest Diptera breeding in fallen fruit. *Journal of Animal Ecology* 54, 507–518.

Atsatt, P.R. (1981) Lycaenid butterflies and ants: selection for enemy-free space. *The American Naturalist* 118, 638–654.

Atwal, A.S. and Sethi, S.L. (1963) Predation by *Coccinella septempunctata* L. on the cabbage aphid, *Lipaphis erysimi* (Kalt.) in India. *Journal of Animal Ecology* 32, 481– 488.

Augspurger, C.K. (1980) Mass-flowering of a tropical shrub (*Hybanthus prunifolius*): influence of pollinator attraction and movement. *Evolution* 34, 475–488.

Auslander, D.M., Oster, G.F. *et al.* (1974) Dynamics of interacting populations. *Journal of the Franklin Institute* 297, 345–376.

Austin, A.D. and Dowton, M. (eds.) (2000) *Hymenoptera, Evolution, Biodiversity and Biological Control*. Collingswood, Australia: CSIRO.

Avrami, M. (1939) Kinetics of phase change. 1. General theory. *Journal of Chemistry and Physics* 7, 1103–1112.

Awmack, C.S. and Leather, S.R. (2002) Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* 47, 817–844.

Axelrod, R. and Hamilton, W.D. (1981) The evolution of co-operation. *Science* 211, 1390–1396.

Ayali, A., Golenser, E. *et al.* (1996) Flight fuel related differences between solitary and gregarious locusts (*Locusta migratoria migratorioides*). *Physiological Entomology* 21, 1–6.

Azad, A.F. (1990) Epidemiology of murine typhus. *Annual Review of Entomology* 35, 553–569.

Baars, M.A. (1979) Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia* 41, 25–46.

Badenes-Perez, F.R., Shelton, A.M. *et al.* (2004) Evaluating trap crops for diamond back moths, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae). *Journal of Economic Entomology* 97, 1365–1372.

Baerends, G.P. (1941) Fortpflanzungsverhalten und Orientierung der Grabwespen *Ammophila campestris*. *Jur. Tijdschrift voor Entomologie* 84, 1–275.

Baguette, M. and Stevens, V.M. (2003) Local populations and metapopulations are both natural and operational categories. *Oikos* 101, 661–663.

Bailey, N.T.J. (1982) *The Biomathematics of Malaria*. London, UK: Griffin and Co.

Bailey, N.T.J. (1994) *Statistical Methods in Biology*, 3rd edn. Cambridge, UK: Cambridge University Press.

Baird, E., Srinivasan, M.V. *et al.* (2005) Visual control of flight speed in honey bees. *The Journal of Experimental Biology* 208, 3895–3905.

Baker, H.G. (1961) The adaptations of flowering plants to nocturnal and crepuscular insects. *The Quarterly Review of Biology* 36, 64–73.

Baker, H.G. (1970) Evolution in the tropics. *Biotropica* 2, 101–110.

Baker, H.G. and Baker, I. (1973) Amino acids in nectar and their evolutionary significance. *Nature* 241, 543–545.

Baker, R.R. (1968) A possible method of evolution of the migratory habit in butterflies. *Philosophical Transactions of the Royal Society B* 253, 309–341.

Baker, R.R. (1978) *The Evolutionary Ecology of Animal Migration*. London, UK: Hodder and Stoughton.

Baker, R.R. (1983) Insect territoriality. *Annual Review of Entomology* 28, 65–89.

Bale, J.S. (2002) Insects and low temperatures: from molecular biology to distributions and abundance. *Philosophical Transaction of the Royal Society B* 357, 849–862.

Baltensweiler, W. (1964) *Zeiraphera griseana* Hubner (Lepidoptera: Tortricidae) in the European Alps. A contribution to the problem of cycles. *The Canadian Entomologist* 96, 792–800.

Baltensweiler, W. (1993) A contribution to the explanation of the larch bud moth cycles, the polymorphic fitness hypothesis. *Oecologia* 93, 251–255.

Baltensweiler, W. and Fischlin, A. (1988) The larch bud moth in the European Alps. In: Berryman, A (ed.) *Dynamics of Forest Insect Populations: Patterns, Causes and Management Strategies*. New York, New York, USA: Academic Press, pp. 331–351.

Baltensweiler, W., Benz, G. *et al.* (1977) Dynamics of larch bud moth populations. *Annual Review of Entomology* 22, 79–100.

Bandong, J.P. and Litsinger, J.A. (2005) Rice crop stage susceptibility to the rice yellow stem borer *Scirpophaga incertulas* (Walker) (Lepidoptera: Pyralidae). *International Journal of Pest Management* 51, 37–43.

Banerjee, B. (1983) Arthropod accumulation on tea in young and old habitats. *Ecological Entomology* 8, 117–123.

Banks, A.N. and Srygley, R.B. (2003) Orientation by magnetic field in leaf-cutter ants, *Atta colombica* (Hymenoptera: Formicidae). *Ethology* 109, 835–846.

Banks, C.J., Macaulay, E.D.M. *et al.* (1968) Cannibalism and predation by aphids. *Nature* 218, 491.

Banno, H. (1990) Plasticity of size and relative fecundity in the aphidophagous lycaenid butterfly, *Taraka hamada*. *Ecological Entomology* 15, 111–113.

Barari, H., Ferguson, A.W. *et al*. (2005) The separation of two hymenopteran parasitoids, *Tersilochus obscurator* and *Tersilochus microgaster* (Ichneumonidae), of stem-mining pests of winter oilseed rape using DNA, morphometric and ecological data. *Bulletin of Entomological Research* 95, 299–307.

Barber, D.C., Dyke, A. et al. (1999) Forcing of the cold event of 8200 years ago by catastrophic drainage of the Laurentide lakes. *Nature* 400, 344–348.

Barbosa, P. (ed) (1998) *Conservation Biological Control*. San Diego, California, USA: Academic Press.

Barbosa, P., Martinat, P. *et al*. (1986) Development, fecundity and survival of the herbivore *Lymantria dispar* and the number of plant species in its diet. *Ecological Entomology* 11, 1–6.

Barbosa, P., Gross, P. *et al*. (1991) Influence of plant allelochemicals on the tobacco hornworm and its parasitoid, *Cotesia congregata*. *Ecology* 72, 1567–1575.

Barbour, D.A. (1985) Patterns of fluctuation in the pine looper moth *Bupalus piniaria* L. in Britain. In: Bevan, D. and Stoakley, J.T. (eds) *Site characteristics and Population Dynamics of Lepidopteran and Hymenopteran Forest Pests*. London, UK: Her Majesty's Stationery Office, pp. 8–20.

Bardner, R., Fletcher, K.E., *et al*. (1973) Fluctuations in populations of wheat bulb fly (Leptohylemyia coarctata) at Rothamsted. *Annals of Applied Biology* 74, 25–34.

Barker, M.J. and Wilson, R.A. (2010) Cohesion, gene flow, and the nature of species. *The Journal of Philosophy* 107, 61–79.

Barnes, H.F. (1946) *Gall Midges of Economic Importance*, vol. 1. London, UK: Crosby Lockwood.

Barone, J.A. (1998) Host-specificity of folivorous insects in a moist tropical forest. *Journal of Animal Ecology* 67, 400–409.

Barrera, R., Amador, M. *et al*. (2008) Unusual productivity of *Aedes aegypti* in septic tanks and its implications for dengue control. *Medical and Veterinary Entomology* 22, 62–69.

Barrett, A.D.T. and Higgs, S. (2007) Yellow fever: a disease that has yet to be conquered. *Annual Review of Entomology* 52, 209–229.

Barry, R.G. and Chorley, R.J. (1995) *Atmosphere, Weather and Climate*, 6th edn. London, UK: Routledge.

Barth, F.G. (1991) *Insects and Flowers: the Biology of a Partnership*. Princeton, New Jersey, USA: Princeton University Press.

Bartholomew, G.A. and Heinrich, B. (1978) Endothermy in African dung beetles during flight, ball making, and ball rolling. *The Journal of Experimental Biology* 73, 65–83.

Barton, N.H. (2001) The role of hybridisation in evolution. *Molecular Ecology* 10, 551–568.

Barton, N.H. and Hewitt, G.M. (1985) Analysis of hybrid zones. *Annual Review of Ecology and Systematics* 16, 113–148.

Barwell, L.J., Isaac, N.J. et al. (2015) Measuring β-diversity with species abundance data. *Journal of Animal Ecology* 84, 1112–1122.

Bascompte, J., Jordano. P., *et al*. (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312, 431–433.

Bateman, A.J. (1948) Intra-sexual selection in *Drosophila*. *Heredity* 2, 349–368.

Bateman, M.A. (1972) The ecology of fruit flies. *Annual Review of Entomology* 17, 493–518.

Bateman, R.P. and Alves, R.T. (2000) Delivery systems for mycoinsecticides using oil-based formulations. *Aspects of Applied Biology* 57, 163–170.

Bateson, W. (1909) Heredity and variation in modern lights. In: Seward, A.C. (ed.) *Darwin and Modern Science*. Cambridge, UK: Cambridge University Press, pp. 85–101.

Batista, P.D., Keddie, B.A. *et al*. (2010) Phylogenetic placement and evidence for horizontal transfer of *Wolbachia* in *Plutella xylostella* (Lepidoptera: Plutellidae) and its parasitoid, *Diadegma insulare* (Hymenoptera: Ichneumonidae). *The Canadian Entomologist* 142, 57–64.

Baumann, P. (2005) Biology of bacteriocyte-associated endosymbionts of plant sap-sucking insects. *Annual Review of Microbiology* 59, 155–189.

Baumhover, A.H., Graham, A.J. *et al*. (1955) Screwworm control through release of sterilized flies. *Journal of Economic Entomology* 48, 462–466.

Bawin, T., Dujeu., D. *et al*. (2016) Ability of *Tuta absoluta* (Lepidoptera: Gelechiidae) to develop on alternative host plant species. *The Canadian Entomologist* 148, 434–442.

Bazzaz, F.A. (1990) The response of natural ecosystems to the rising global CO2 levels. *Annual Review of Ecology and Systematics* 21, 167–196.

Beaver, R.A. (1966) The development and expression of population tables for the bark beetle *Scolytus scolytus* (F.). *Journal of Animal Ecology* 35, 27–41.

Beaver, R.A. (1967) The regulation of population density in the bark beetle *Scolytus scolytus* (F.). *Journal of Animal Ecology* 36, 435–451.

Beaver, R.A. (1973) The effects of larval competition on puparial size in *Sarcophaga* spp. (Diptera: Sarcophagidae) breeding in dead snails. *Journal of Entomology A* 48, 1–9.

Beaver, R.A. (1979) Non-equilibrium "island" communities, a guild of tropical bark beetles. *Journal of Animal Ecology* 48, 987–1002.

Beck, S.D. (1980) *Insect Photoperiodism*. New York, New York, USA: Academic Press.

Becker, N., Pedrić, D. *et al.* (2010) *Mosquitoes and Their Control*. New York, New York, USA: Springer.

Beddington, J.R. (1975) Mutual interference between searching parasitoids or predators and its effect on searching efficiency. *Journal of Animal Ecology* 44, 331–340.

Beddington, J.R., Free, C.A. *et al.* (1975) Dynamic complexity in predator-prey models framed in simple difference equations. *Nature* 225, 58–60.

Bedford, G.O. (2013) Biology and management of palm dynastid beetles: recent advances. *Annual Review of Entomology* 58, 353–372.

Beeson, C.F.C. (1941) *The Ecology and Control of the Forest Insects of India and the Neighbouring Countries*. Reprinted 1961. New Delhi, India: Government of India.

Begon, M. (1976) Dispersal, density and microdistribution in *Drosophila subobscura* Collin. *Journal of Animal Ecology* 45, 441–456.

Begon, M. (1983) Grasshopper populations and weather: the effects of insolation on *Chorthippus brunneus*. *Ecological Entomology* 8, 361–370.

Begon, M. Harper, J.L., *et al.* (1996a) *Ecology*, 3rd edn. Oxford, UK: Blackwell.

Begon, M., Mortimer, M. *et al.* (1996b) *Population Ecology*, 3rd edn. Cambridge, UK: Blackwell Science.

Behle, R.W., Hibbard, B.E. *et al.* (2008) Examining *Cuphea* as a potential host for western corn rootworm (Coleoptera: Chrysomelidae): larval development. *Journal of Economic Entomology* 101, 797–800.

Beirão, M.V., Campos-Neto, F.C. *et al.* (2012) Population biology and natural history of *Parides burchellanus* (Papilionidae: Triodini), an endangered Brazilian butterfly. *Annals of the Entomological Society of America* 105, 36–43.

Beldade P., Koops, K. *et al.* (2002) Developmental constraints versus flexibility in morphological evolution. *Nature* 416, 844–847.

Bell, J.R., Bohan, D.A. *et al.* (2005) Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research* 95, 69–114.

Bellows, T.S. and Fisher, T.W. (1999) *Handbook of Biological Control*. London, UK: Academic Press.

Bellows, T.S., van Driesche, R.G. *et al.* (1992) Life-table construction and analysis in the evaluation of natural enemies. *Annual Review of Entomology* 37, 587–614.

Benlarbi, M. and Ready, P.D. (2003) Host-specific *Wolbachia* strains in widespread populations of *Phlebotomus perniciosus* and *P. papatasi* (Diptera: Psychodidae), and prospects for driving genes into these vectors of *Leishmania*. *Bulletin of Entomological Research* 93, 383–391.

Bennett, A.F. (1991) The evolution of activity capacity. *The Journal of Experimental Biology* 160, 1–23.

Bennett, F.D. (1965) Notes on a nest of *Eulaema terminata* Smith (Hymenoptera, Apoidea). *Insectes Sociaux* 12, 81–92.

Ben-Shahar, Y. *et al.* (2002) Genetics of gene action across different time scales on behavior. *Science* 296, 741–744.

Ben-Shlomo, R., Motro, U. *et al.* (1991) The influence of the ability to disperse on generation length and population size in the flour beetle, *Tribolium castaneum*. *Ecological Entomology* 16, 279–282.

Benton, T.G., Plaistow, S.J. *et al.* (2006) Complex population dynamics and complex causation: devils, details and demography. *Proceedings of the Royal Society B* 273, 1173–1181.

Bentz, B.J., Logan, J.A. *et al.* (2001) Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size. *The Canadian Entomologist* 133, 375–387.

Berec, L., Angulo, E. *et al.* (2006) Multiple Allee Effects and population management. *Trends in Ecology and Evolution* 22, 185–191.

Berenbaum, M.R. (1995) Turnabout is fair play: Secondary roles for primary compounds. *Journal of Chemical Ecology* 21, 925–940.

Berenbaum, M.R. (1999) Shelter-making caterpillars: rolling their own. *Wings* 22, 7–10.

Beres, B.L., Dosdall, L.M. *et al.* (2011) Biology and integrated management of wheat stem sawfly and the need for continuing research. *The Canadian Entomologist* 143, 105–125.

Bergelson, J. and Purrington, C.B. (1996) Surveying patterns in the cost of resistance in plants. *The American Naturalist* 14, 536–558.

Berger, D., Walters, R. *et al.* (2008) What limits insect fecundity? Body size- and temperature-dependent egg maturation and oviposition in a butterfly. *Functional Ecology* 22, 523–529.

Bergh, J.C., Leskey, T.C. *et al.* (2009) Dogwood borer (Lepidoptera: Sesiidae) abundance and seasonal flight activity in apple orchards, urban landscapes, and woodlands in five eastern states. *Environmental Entomology* 38, 530–538.

Berland, L. (1935) Premiers résultats de mes recherches en avion sur la faune et la flore atmosphériques. *Annales - Société Entomologique de France* 104, 73–96.

Berlocher, S.H. and Feder, J.L. (2002) Sympatric speciation in phytophagous insects: moving beyond controversy? *Annual Review of Entomology* 47, 773–815.

Bernal, C.C., Aguda, R.M. *et al.* (2002) Effect of rice lines transformed with *Bacillus thuringiensis* toxin genes on the brown planthopper and its predator *Cyrtorhinus lividipennis*. *Entomologia Experimentalis et Applicata* 102, 21–28.

Bernays, E.A. and Chapman, R.F. (1994) *Host-plant Selection by Phytophagous Insects*. New York, New York, USA: Chapman and Hall.

Bernays, E.A. and Graham, M. (1988) On the evolution of host specificity in phytophagous arthropods. Ecology 69, 886–892.

Bernays, E.A., Edgar, J.A. *et al.* (1977) Pyrrolizidine alkaloids sequestered and stored by the aposematic grasshopper *Zonocerus variegatus*. *Journal of Zoology* 182, 85–87.

Berry, A.J. and Willmer, P.G. (1986) Temperature and the colour polymorphism of *Philaenus spumarius* (Homoptera: Aphrophoridae). *Ecological Entomology* 11, 251–259.

Berry, R.J. (1985) The processes of pattern: genetical possibilities and constraints in coevolution. *Oikos* 44, 222–228.

Berryman, A.A. (1973) Population dynamics of the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). 1. Analysis of population behaviour and survival from 1964 to 1971. *The Canadian Entomologist* 105, 1465–1488.

Berryman, A.A. (1986) *Forest Insects - Principles and Practice of Population Management*. New York, New York, USA: Plenum Press.

Berryman, A.A. (1988) (ed.) *Dynamics of Forest Insect Populations*. New York, New York, USA: Plenum Press.

Berryman, A.A. (1991a) Vague notions of density dependence. *Oikos* 62, 252–254.

Berryman, A.A. (1991b) Population theory: an essential ingredient in pest prediction, management and policy making. *American Entomologist* 37, 138–142.

Berryman, A.A. (1992) The origins and evolution of predator-prey theory. *Ecology* 73, 1530–1535.

Berryman, A.A. (1996) What causes population cycles of forest Lepidoptera? *Trends in Ecology and Evolution* 11, 28–32.

Berryman, A.A. (1999) *Principles of Population Dynamics and their Application*. Cheltenham, UK: Stanley Thornes.

Berryman, A.A. (2002) Population: a central concept for ecology? *Oikos* 97, 439–442.

Berryman, A.A. (2003) On principles, laws and theory in population ecology. *Oikos* 103, 695–701.

Berryman, A.A. and Chen, X. (1999) Population cycles: the relationship between cycle period and reproductive rate depends on the relative dominance of bottom-up and top-down control. *Oikos* 87, 589–593.

Berryman, A.A. and Turchin, P. (2001) Identifying the density-dependent structure underlying ecological time series. *Oikos* 92, 265–270.

Berwaerts, K., Van Dyck, H. *et al.* (2002) Does flight morphology relate to flight performance? An experimental test with the butterfly *Pararge aegeria*. *Functional Ecology* 16, 484–491.

Besterman, E.M.M. (1988) Robert Jackson, M.D. 1750–1827. Sometime doctor in Jamaica and a bold crusader of his day. *Jamaica Journal* 20, 51–54.

Betts, E. (1976) Forecasting infestations of tropical migrant pests: the desert locust and the African armyworm. *Symposia of the Royal Entomological Society* 7, 113–134.

Betts, M.M. (1955) The food of titmice in oak woodland. *Journal of Animal Ecology* 24, 282–323.

Bezemer, T.M., Wagenaar, R. *et al.* (2003) Interactions between above- and belowground insect herbivores as mediated by the plant's defence system. *Oikos* 101, 555–562.

Bigger, M. (1973) An investigation by Fourier Analysis into the interaction between coffee leaf-miners and their larval parasites. *Journal of Animal Ecology* 42, 417–434.

Bigler, F. (1989) Quality assessment and control in entomophagous insects used for biological control. *Journal of Applied Entomology* 108, 390–400.

Bingham, R.A. and Orthner, A.R. (1998) Efficient pollination of alpine plants. *Nature* 391, 238–239.

Birch, L.C. (1948) The intrinsic rate of natural increase in an insect population. *Journal of Animal Ecology* 17, 15–26.

Birch, L.C. (1957) The meanings of competition. *The American Naturalist* 91, 5–18.

Birch, L.C. (1960) The genetic factor in population ecology. *The American Naturalist* 94, 5–24.

Bird, J.M. and Hodkinson, I.D. (2005) What limits the altitudinal distribution of *Craspedolepta* species (Sternorrhyncha: Psylloidea) on fireweed? *Ecological Entomology* 30, 510–520.

Birley, M.H. (1977) The estimation of insect density and instar survivorship functions from census data. *Journal of Animal Ecology* 46, 495–510.

Bishop, J.A. and Cook, L.M. (1975) Moths, melanism and clean air. *Scientific American* 232, 90–99.

Bjerknes, J. (1969) Atmospheric teleconnections from the equatorial Pacific. *Monthly Weather Review* 97, 163–172.

Björklund, M. (1997) Are "comparative methods" always necessary? *Oikos* 80, 607–612.

Bjornstad, O.N. and Hansen, T.F. (1994) Individual variation and population dynamics. *Oikos* 69, 167–171.

Bjornstad, O.N., Peltonen, M. *et al.* (2002) Waves of larch budmoth outbreaks in the European Alps. *Science* 298, 1020–1023.

Blackburn, M.B., Farrar, R.R. *et al.* (2006) Remarkable susceptibility of the diamondback moth (*Plutella xylostella*) to ingestion of Pir toxins from *Photorhabdus luminescens*. *Entomologia Experimentalis et Applicata* 121, 31–37.

Blackburn, T.M. and Gaston, K.J. (1999) The relationship between animal abundance and body size: a review of the mechanisms. *Advances in Ecological Research* 28, 181–210.

Blackman, R.L. and Eastop, V.F. (2000) *Aphids on the World's Crops*, 2nd edn. London, UK: Natural History Museum/Wiley.

Blackshaw, R.P. (1987) The use of water traps for crane fly monitoring: an assessment of operator efficiency. *Annals of Applied Biology* 110, 239–245.

Blackshaw, R.P. (1988) Effects of cultivations and previous cropping on leatherjacket populations in spring barley. *Research and Development in Agriculture* 5, 35–37.

Blandin, S.A., Wang-Sattler, R. *et al.* (2009) Dissecting the genetic basis of resistance to malarial parasites in *Anopheles gambiae*. *Science* 326, 147–150.

Blaustein, L. and Margalit, J. (1994) Mosquito larvae (*Culiseta longiareolata*) prey upon and compete with toad tadpoles (*Bufo viridis*). *Journal of Animal Ecology* 63, 841–850.

Blest, A.D. (1957) The function of eyespot patterns in the Lepidoptera. *Behaviour* 11, 209–255.

Blommers, L.H.M. (1994) Integrated pest management in European apple orchards. *Annual Review of Entomology* 39, 213–241.

Blows, M.W. and Hoffmann, A.A. (2005) A reassessment of genetic limits to evolutionary change. *Ecology* 86, 1371–1384.

Blum, M.S. (1979) *The Chemical Defences of Arthropods*. New York, New York, USA: Academic Press.

Bodenheimer, F.S. (1928) Welche Faktoren regulieren die Individuenzahl einer Insektenart in der Natur? *Biologisches Zentralblatt* 48, 714–739.

Boggs, C.L. (1995) Male nuptial gifts: Phenotypic consequences and evolutionary implications. In Leather, S.R. and Hardie, J. (eds) *Insect Reproduction*. Boca Raton: CRC Press, 215–242.

Boggs, C.L. (1997) Reproductive allocation from reserves and income in butterfly species with differing adult diets. *Ecology* 78, 181–191.

Boggs, C.L. and Gilbert, L.E. (1979) Male contribution to egg production in butterflies: evidence for transfer of nutrients at mating. *Science* 206, 83–84.

Boggs, C.L. and Jackson, L.A. (1991) Mud puddling by butterflies is not a simple matter. *Ecological Entomology* 16, 123–127.

Boiteau, G. (1988) Sperm utilisation and post-copulatory female-guarding in the Colorado potato beetle, *Leptinotarsa decemlineata*. *Entomologia Experimentalis et Applicata* 47, 183–187.

Boiteau, G. and Coleman, W. (1996) Cold tolerance in the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). *The Canadian Entomologist* 128, 1087–1099.

Boiteau, G. and Colpitts, B. (2004) The potential of portable harmonic radar technology for the tracking of beneficial insects. *International Journal of Pest Management* 50, 233–242.

Boiteau, G., Picka, J.D. *et al.* (2008) Potato field colonization by low-density populations of Colorado potato beetle as a function of crop rotation distance. *Journal of Economic Entomology* 101, 1575–1583.

Boller, E.F. and Prokopy, R.J. (1976) Bionomics and management of *Rhagoletis*. *Annual Review of Entomology* 21, 223–246.

Bolnick, D.I. and Fitzpatrick, B.M. (2007) Sympatric speciation: models and empirical evidence. *Annual Review of Ecology, Evolution and Systematics* 38, 459–487.

Bolnick, D.I., Svanbäck, R. *et al.* (2003) The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist* 161, 1–28.

Bonal, R., Muñoz, A. *et al.* (2010) Mismatch between the timing of oviposition and the seasonal optimum. The stochastic phenology of Mediterranean acorn weevils. *Ecological Entomology* 35, 270–278.

Bond, A.B. (2007) The evolution of color polymorphism: crypticity, searching images, and apostatic selection. *Annual Review of Ecology, Evolution and Systematics* 38, 489–514.

Bond, G., Kromer, B. *et al.* (2001) Persistent solar influence on the North Atlantic climate during the Holocene. *Science* 294, 2130–2135.

Bond, J.G., Marina, C.F. *et al.* (2004) The naturally derived insecticide spinosad is highly toxic to *Aedes* and *Anopheles* mosquito larvae. *Medical and Veterinary Entomology* 18, 50–56.

Bonduriansky, R. and Day, T. (2009) Nongenetic inheritance and its evolutionary implications. *Annual Review of Ecology, Evolution and Systematics* 40, 103–125.

Bonhomme, R. (2000) Bases and limits to using “degree-day” units. *European Journal of Agronomy* 13, 1–10.

Bonnemaison, L. (1951) Contribution a la étude des facteurs provoquant l’apparition des formes ailées et sexuées chez les Aphidinae. *Annales Épiphytes, Serie C* 2, 1–380.

Bonsall, M.B. and Hassell, M.P. (1997) Apparent competition structures ecological assemblages. *Nature* 388, 371–373.

Bonsall, M.B. and Hassell, M.P. (1998) Population dynamics of apparent competition in a host-parasitoid assemblage. *Journal of Animal Ecology* 67, 918–929.

Bopp, S. and Gottsberger, G. (2004) Importance of *Silene latifolia* ssp. *alba* and *S. dioica* (Caryophillaceae) as host plants of the parasitic pollinator *Hadena bicruris* (Lepidoptera; Noctuidae). *Oikos* 105, 221–228.

Boppré, M., Vane-Wright, R.I. *et al.* (2017) A hypothesis to explain accuracy of wasp resemblances. *Ecology and Evolution* 7, 73–81.

Bordbar, A., Soleimani, S. *et al.* (2014) Three strains of *Wolbachia pipientis* and high rates of infection in Iranian sand fly species. *Bulletin of Entomological Research* 104, 195–202.

Borror, D.J., Triplehorn, *et al.* (1989) *An Introduction to the Study of Insects*, 6th edn. New York, New York, USA: Saunders.

Bottrell, D.G. and Adkisson, P.L. (1977) Cotton insect pest management. *Annual Review of Entomology* 22, 451–481.

Boucher, T.J., Ashley, R. *et al.* (2003) managing the pepper maggot (Diptera: Tephritidae) using perimeter trap cropping. *Journal of Economic Entomology* 96, 420–432.

Boulanger, Y. and Arsenault, D. (2004) Spruce budworm outbreaks in eastern Quebec over the last 450 years. *Canadian Journal of Forest Research* 34, 1035–1043.

Bouletreau, M. (1986) The genetic and coevolutionary interactions between parasitoids and their hosts. In: Waage, J.K. and Greathead, D.J. (eds) *Insect Parasitoids*. London, UK: Academic Press, pp. 169–200.

Bourchier, R.S. and Smith, S.M. (1996) Influence of environmental conditions and parasitoid quality on field performance of *Trichogramma minutum*. *Entomologia Experimentalis et Applicata* 80, 461–468.

Bowen, D., Rocheleau, T.A. *et al.* (1998) Insecticidal toxins from the bacterium *Photorhabdus luminescens*. *Science* 280, 2129–2132.

Bowen, M.F. (1991) The sensory physiology of host-seeking behavior in mosquitoes. *Annual Review of Entomology* 36, 139–158.

Box, H.E. (1953) *List of Sugar-Cane Insects*. London, UK: Commonwealth Institute of Entomology.

Boyer, S., Zhang., H. *et al.* (2012) A review of control methods and resistance mechanisms in stored-product insects. *Bulletin of Entomological Research* 102, 213–229.

Brackenbury, J.H. (1995) *Insects in Flight*. London, UK: Cassel.

Bradshaw, A.D. (1987) Comparison – its scope and limits. *New Phytologist* 106 (Suppl.), 3–21.

Bradshaw, A.D. (1991) Genostasis and the limits to evolution. *Philosophical Transactions of the Royal Society B* 333, 289–305.

Bradshaw, W.E. and Holzapfel, C.M. (1991) Fitness and habitat segregation of British tree-hole mosquitoes. *Ecological Entomology* 16, 133–144.

Brady, E. (2003) *Aesthetics of the Natural Environment*. Edinburgh: Edinburgh University Press.

Braimah, H. and van Emden, H.F. (1999) Evidence for the presence of chemicals attractive to the banana weevil, *Cosmopolites sordidus* (Coleoptera: Curculionidae) in dead banana leaves. *Bulletin of Entomological Research* 89, 485–491.

Brakefield, P.M., Gates, J. *et al.* (1996) Development, plasticity and evolution of butterfly eyespot patterns. *Nature* 384, 236–242.

Bray, F. (1986) *The Rice Economies*. Oxford, UK: Blackwell.

Bray, J.R. and Gorham, E. (1964) Litter production in forests of the world. *Advances in Ecological Research* 2, 101–157.

Bressan, A., Larrue, J. *et al.* (2006) patterns of phytoplasma-infected and infective *Scaphoideus titanus* leafhoppers in vineyards with a high incidence of Flavescens dorée. *Entomologia Experimentalis et Applicata* 119, 61–69.

Brewbaker, J.L. (1957) Pollen cytology and self-incompatibility systems in plants. *Journal of Heredity* 48, 271–277.

Brewer, A.M. and Gaston, K.J. (2003) The geographical range structure of the holly leaf-miner. 2. Demographic rates. *Journal of Animal Ecology* 72, 82–93.

Brewer, M.J. and Elliot, N.C. (2004) Biological control of cereal aphids in North America and mediating effects of host plant and habitat modifications. *Annual Review of Entomology* 49, 219–242.

Bridges, J.R. and Moser, J.C. (1983) Role of two phoretic mites in transmission of bluestain fungus, *Ceratocystis minor*. *Ecological Entomology* 8, 9–12.

Bridle, J.R. and Vines, T.H. (2006) Limits to evolution at range margins: when and why does adaptation fail? *Trends in Ecology and Evolution* 22, 140–147.

Bridle, J.R., Gavaz, S. *et al.* (2009) Testing limits to adaptation along altitudinal gradients in rainforest *Drosophila*. *Proceedings of the Royal Society B* 276, 1507–1515.

Briggs, C.J. and Latto, J. (2000) The effect of dispersal on the population dynamics of a gall-forming midge and its parasitoids. *Journal of Animal Ecology* 69, 96–105.

Brindley, T.A., Sparks, A.N. *et al.* (1975) Recent research advances on the European corn borer in North America. *Annual Review of Entomology* 20, 221–239.

Briscoe, A.D. and Chittka, L. (2001) The evolution of color vision in insects. *Annual Review of Entomology* 46, 471–510.

Broadie, K.S. and Bradshaw, W.E. (1991) Mechanisms of interference competition in the western tree-hole mosquito, *Aedes sierrensis*. *Ecological Entomology* 16, 145–154.

Brockmann, H.J. (1992) Male behavior, courtship and nesting in *Trypoxylon* (*Trypargilum*) *monteverdeae* (Hymenoptera: Sphecidae). *Journal of the Kansas Entomological Society* 65, 66–84.

Brodsky, A.K. (1994) *The Evolution of Insect Flight*. Oxford, UK: Oxford University Press.

Bronstein, J.L. (1998) The contribution of ant-plant protection studies to our understanding mutualism. *Biotropica* 30, 150–161.

Brook, B.W. and Bradshaw, C.J.A. (2006) Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* 87, 1445–1451.

Brower, L.P. (1984) Chemical defence in butterflies. In: Vane-Wright, R.I. and Ackery, P.R. (eds) *The Biology of Butterflies*. Symposium of the Royal Entomological Society of London, No. 11. London, UK: Academic Press, pp. 109–134.

Brown, C.E. (1965) Mass transport of forest tent caterpillar moths, *Malacosoma disstria* Hübner, by a cold front. *The Canadian Entomologist* 97, 1073–1075.

Brown, D., Alexander, N.D.E. *et al.* (1993) Structured accounting of the variance of demographic change. *Journal of Animal Ecology* 62, 490–502.

Brown, E.S. (1951) The relationship between migration rate and type of habitat in aquatic insects, with special reference to certain species of Corixidae. *Proceedings of the Zoological Society of London* 121, 539–545.

Brown, E.S. (1965) Notes on the migration and direction of flight of *Eurygaster* and *Aelia* species (Hemiptera, Pentatomoidea) and their possible bearing on invasions of cereal crops. *Journal of Animal Ecology* 34, 93–107.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *The American Naturalist* 124, 255–279.

Brown, J.H. and Maurer, B.A. (1989) Macroecology: the division of food and space among species on continents. *Science* 243, 1145–1150.

Brown, J.H., Mehlman D. *et al.* (1995) Spatial variation in abundance. *Ecology* 76, 2028–2043.

Brown, J.H., Stevens, G.C. *et al.* (1996) The geographic range: size, shape, boundaries and internal structure. *Annual Review of Ecology and Systematics* 27, 597–623.

Brown, J.K. and Czosnek, H. (2002) Whitefly transmission of plant viruses. *Advances in Botanical Research* 36, 65–100.

Brown, J.K., Frohlich, D.R. *et al.* (1995) The sweet potato or silver leaf whiteflies: biotypes of *Bemisia tabaci* or a species complex? *Annual Review of Entomology* 40, 511–534.

Brown, S.E., Been, B.O. *et al.* (2006) Detection and variability of the lethal yellowing group (16Sr IV) phytoplasmas in the *Cedusa* sp. (Hemiptera: Auchenorrhyncha: Derbidae) in Jamaica. *Annals of Applied Biology* 149, 53–62.

Brown, V.K. (1985) Insect herbivores and plant succession. *Oikos* 44, 17–22.

Brown, V.K. and Gange, A.C. (1990) Insect herbivory below ground. *Advances in Ecological Research* 20, 1–58.

Brownlee, J. (1919) Notes on the biology of a life-table. *Journal of the Royal Statistical Society* 82, 32–65.

Bruck, D.J., Edwards, D.L. *et al.* (2008) Susceptibility of strawberry crown moth (Lepidoptera: Sesiidae) to entomopathogenic nematodes. *Journal of Economic Entomology* 101, 251–255.

Brues, C.T. (1946) Insect Dietary. Cambridge, Massachusetts, USA: Harvard University Press.

Brumpt, E. (1912) Le *Trypanosoma cruzi* evolue chez *Conorhinus megistus*, *Cimex lectularis*, *Cimex boueti*, *Ornithodorus moubata*. Cycle évolutif de ce parasite. *Bulletin Société Pathologie Exotique* 5, 360–367.

Brussard, P.F. (1984) Geographic patterns and environmental gradients: the central-marginal model in *Drosophila* revisited. *Annual Review of Ecology and Systematics* 15, 25–64.

Brust, G.E. (1994) Natural enemies in straw mulch reduce Colorado potato beetle populations and damage in potato. *Biological Control* 4, 163–169.

Bryant, E.H. (1969) A system favoring the evolution of holometabolous development. *Annals of the Entomological Society of America* 62, 1087–1091.

Bryant, E.H. (1974) On the adaptive significance of enzyme polymorphisms in relation to environmental variability. *The American Naturalist* 108, 1–19.

Buchmann, S.L. and Nabhan, G.P. (1996) *The Forgotten Pollinators*. Covelo, California, USA: Island Press.

Bullini, L. (1994) Origin and evolution of animal hybrid species. *Trends in Ecology and Evolution* 9, 422–426.

Bulmer, M.G. (1975) The statistical analysis of density dependence. *Biometrics* 31, 901–911.

Bultman, T.L. and Faeth, S.H. (1988) Abundance and mortality of leaf miners on artificially shaded Emory oak. *Ecological Entomology* 13, 131–142.

Bürger, R. (1999) Evolution of genetic variability and the advantage of sex and recombination in changing environments. *Genetics* 153, 1055–1069.

Bürger, R., Schneider, K.A. *et al.* (2006) The conditions for speciation through intraspecific competition. *Evolution* 60, 2185–2206.

Burgess, I.F. (2004) Human lice and their control. *Annual Review of Entomology* 49, 457–481.

Burke, J.M. and Arnold, M.L. (2001) Genetics and the fitness of hybrids. *Annual Review of Genetics* 35, 31–52.

Burkness, E.C. and Hutchison, W.D. (2008) Implementing reduced-risk integrated pest management in fresh-market cabbage: improved net returns via scouting and timing of effective control. *Journal of Economic Entomology* 101, 461–471.

Burnett, T. (1949) The effect of temperature on a host-parasite population. *Ecology* 30, 113–134.

Burrack, H.J., Fornell, A.M. *et al.* (2009) Intraspecific larval competition in the olive fruit fly (Diptera: Tephritidae). *Environmental Entomology* 38, 1400–1410.

Burrough, P.A. (1981) Fractal dimensions of landscapes and other data. *Nature* 294, 240–242.

Burt, A. (1995) The evolution of fitness. *Evolution* 49, 1–8.

Burt, A. (2000) Natural selection in the wild. *Trends in Ecology and Evolution* 15, 306–307.

Burt, A. (2003) Site-specific selfish genes as tools for the control and genetic engineering of natural populations. *Proceedings of the Royal Society B* 270, 921–928.

Burt, A. and Trivers, R.L. (2006) *Genes in Conflict*. Cambridge, Massachusetts, USA: Harvard University Press.

Burt, P.G.A. and Pedgley, D.E. (1997) Nocturnal insect migrations: effect of local winds. *Recent Advances in Ecological Research* 27, 61–92.

Busck, A. (1912) On the rearing of *Dermatobia hominis* Linnaeus. *Proceedings of the Entomological Society of Washington* 14, 9–12.

Bush, G.L. (1969) Sympatric host race formation and speciation in frugivorous flies of the genus Rhagoletis (Diptera: Tephritidae). *Evolution* 23, 237–251.

Bush, G.L. (1994) Sympatric speciation in animals: new wine in old bottles. *Trends in Ecology and Evolution* 9, 285–288.

Bushing, R.W. (1965) A synoptic list of the parasites of the Scolytidae (Coleoptera) in North America north of Mexico. *The Canadian Entomologist* 97, 449–492.

Bushland, R.C. and Hopkins, D.E. (1953) Sterilization of screw-worm flies with X-rays and gamma-rays. *Journal of Economic Entomology* 46, 648–656.

Butts, R.A. and Schaalje, G.B. (1997) Impact of subzero temperatures on survival, longevity, and natality of adult Russian wheat aphids (Homoptera: Aphididae). *Environmental Entomology* 26, 661–667.

Buxton, P.A. (1923) *Animal Life in Deserts*. London, UK: Edward Arnold.

Buxton, P.A. (1955) The natural history of tsetse flies. An account of the biology of the genus *Glossina* (Diptera). London, UK: H.K. Lewis & Co. Ltd.

Byers, G.W. (1961) The crane fly genus *Dolichopeza* in North America. *University of Kansas Science Bulletin* 42, 665–924.

Byers, J.A. (1992) Dirichlet tessellations of bark beetle spatial attack points. *Journal of Animal Ecology* 61, 759–768.

Cahenzli, F. and Erhardt, A. (2013) Nectar amino acids enhance reproduction in male butterflies. *Oecologia* 171, 197–205.

Caley, M.J. and Schluter, D. (1997) The relationship between local and regional diversity. *Ecology* 78, 70–80.

Callaghan, T.V., Carlsson, B.A. *et al.* (1992) Clonal plants and environmental change: introduction to the proceedings and summary. *Oikos* 63, 341–347.

Caltagirone, L.E. (1981) Landmark examples in classical biological control. *Annual Review of Entomology* 26, 213–232.

Caltagirone, L.E. and Doutt, R.L. (1989) The history of the *Vedalia* beetle importation to California and its impact on the development of biological control. *Annual Review of Entomology* 34, 1–16.

Camacho, J.P.M., Sharbel, T.F. *et al.* (2000) B-chromosome evolution. *Philosophical Transactions of the Royal Society B* 355, 163–178.

Camargo, A.P. (1999) Phytomonas and other trypanosomatid parasites of plants and fruit. *Advances in Parasitology* 42, 29–112.

Cameron, G.R. (1945) Risks to man and animals from the use of DDT. *British Medical Journal* 3, 783–785.

Cameron, R.A.D. and Redfern, M. (1978) Population dynamics of two hymenopteran parasites of the yew gall midge *Taxomyia taxi* (Inchbald). *Ecological Entomology* 3, 265–272.

Cameron, S.A. (2004) Phylogeny and biology of Neotropical orchid bees (Euglossini). *Annual Review of Entomology* 49, 377–404.

Cammell, M.E. and Knight, J.D. (1992) Effects of climatic change on the population dynamics of crop pests. *Advances in Ecological Research* 22, 117–162.

Campbell, A., Frazer, B.D. *et al.* (1974) Temperature requirements of some aphids and their parasites. *Journal of Applied Ecology* 11, 431–438.

Campbell, R.W. and Sloan, R.J. (1976) Influence of behavioral evolution on gypsy moth pupal survival in sparse populations. *Environmental Entomology* 5, 1211–1217.

Campbell, S.A. and Borden, J.H. (2005) Bark reflectance spectra of conifers and angiosperms: implications for host discrimination by coniferophagous bark and timber beetles. *The Canadian Entomologist* 137, 719–722.

Cane, M.A. (1986) El Niño. *Annual Review of Earth and Planetary Science* 14, 43–70.

Cappuccino, N. and Kareiva, P. (1985) Coping with a capricious environment: a population study of a rare pierid butterfly. *Ecology* 66, 152–162.

Cárcamo, H.A., Herle, C.E. *et al*. (2009) Cold hardiness and overwintering survival of cabbage seed pod weevil, *Ceutorhynchus obstrictus*. *Entomologia Experimentalis et Applicata* 133, 223–231.

Cardé, R.T. (1996) Odour plumes and odour-mediated flight in insects. In: Bock, R.G. and Cardew, G. (eds) *Olfaction in Mosquito-Host Interactions*. Chichester, UK: Wiley, pp. 54–70.

Cardé, R.T. and Minks, A.K. (1995) Control of moth pests by mating disruption: successes and constraints. *Annual Review of Entomology* 40, 559–585.

Cardé, R.T. and Willis, M.A. (2008) Navigational strategies used by insects to find distant, wind-borne sources of odor. *Journal of Chemical Ecology* 34, 854–866.

Carey, J.R. (1989) The multiple decrement life table: a unifying framework for cause-of-death analysis in ecology. *Oecologia* 78, 131–137.

Carey, J.R. (2001) Insect biodemography. *Annual Review of Entomology* 46, 79–110.

Caron, V. and Myers, J.H. (2008) Positive association between resistance to *Bacillus thuringiensis* and overwintering survival of cabbage loopers, *Trichoplusia ni* (Lepidoptera: Noctuidae). *Bulletin of Entomological Research* 98, 317–322.

Caron, V. and Myers, J.H. *et al*. (2010) The failure to discriminate: superparasitism of *Trichoplusia ni* Hübner by a generalist tachinid parasitoid. *Bulletin of Entomological Research* 100, 255–261.

Carpenter, J.E., Sparks, A.N. *et al*. (1989) *Heliothis zea* (Lepidoptera: Noctuidae): effects of radiation and inherited sterility on mating competitiveness. *Journal of Economic Entomology* 82, 109–113.

Carr, E.H. (1987) *What is History*? London, UK: Penguin.

Carrière, Y., Ellers-Kirk, C. *et al*. (2001) Overwintering cost associated with resistance to transgenic cotton in the pink bollworm (Lepidoptera: Gelechiidae). *Journal of Economic Entomology* 94, 935–941.

Carson, R. (1962) *Silent Spring*. Boston, Massachusetts, USA: Riverside Press.

Carter, J.B. (1976) A survey of microbial, insect and nematode parasites of Tipulidae (Diptera) larvae in north-east England. *The Journal of Applied Ecology* 13, 103–122.

Carter, M.C. and Dixon, A.G.F (1984) Honeydew: an arrestant stimulant for coccinellids. *Ecological Entomology* 9, 383–387.

Carter, R.N. and Prince, S.D. (1981) Epidemic models used to explain biogeographical distribution limits. *Nature* 293, 644–645.

Carter, V., Underhill, A. *et al*. (2013) Killer bee molecules: antimicrobial peptides as effector molecules to target sporogonic stages of *Plasmodium*. *PloS Pathogens* 9(11), e1003790.

Carvell, C., Rothery, P. *et al*. (2008) Effects of resource availability and social parasite invasion on field colonies of *Bombus terrestris*. *Ecological Entomology* 33, 321–327.

Carver, S., Spafford, H. *et al*. (2009) Colonisation of ephemeral water bodies in the wheat belt of Western Australia by assemblages of mosquitoes (Diptera: Culicidae): role of environmental factors, habitat, and disturbance. *Environmental Entomology* 38, 1585–1594.

Casas, J., Driessen, G. *et al*. (2003) Energy dynamics in a parasitoid foraging in the wild. *Journal of Animal Ecology* 72, 691–697.

Casas, J., Pincebourde, S. *et al*. (2005) Lifetime nutrient dynamics reveal simultaneous capital and income breeding in a parasitoid. *Ecology* 86, 545–554.

Casey, T.M. (1976) Flight energetics of sphinx moths: power input during hovering flight. *Journal of Experimental Biology* 64, 529–543.

Casey, T.M., May, M.L. *et al*. (1985) Flight energetics of euglossine bees in relation to morphology and wing stroke frequency. *The Journal of Experimental Biology* 116, 271–289.

Casida, J.E. and Quistad, G.B. (1998) Golden age of insecticide research: past, present or future? *Annual Review of Entomology* 43, 1–16.

Casper, B.B. and Jackson, R.B. (1997) Plant competition underground. *Annual Review of Ecology and Systematics* 28, 545–570.

Caswell, H. (1978) Predator-mediated coexistence: a non-equilibrium model. *The American Naturalist* 112, 127–154.

Caswell, H. (2000) *Matrix Population Models: Construction, Analysis and Interpretation*, 2nd edn. Sunderland, Massachusetts, USA: Sinauer Associates.

Caswell, H. and Reed, F. (1975) Indigestibility of C_4 bundle sheath cells by the grasshopper *Melanoplus confusus*. *Annals of the Entomological Society of America* 68, 686–688.

Cates, R.G. and Orions, G.H. (1975) Successional status and the palatability of plants to generalised herbivores. *Ecology* 56, 410–418.

Catts, E.P. and Goff, M.L. (1992) Forensic entomology in criminal investigations. *Annual Review of Entomology* 37, 253–273.

Cazelles, B., Chavez, M. *et al.* (2008) Wavelet analysis of ecological time series. *Oecologia* 156, 287–304.

Ceccato, P., Cressman, K. *et al.* (2007) The desert locust upsurge in West Africa (2003–2005): information on the desert locust early warning system and the prospects for seasonal climate forecasting. *International Journal of Pest Management* 53, 7–13.

Chadee, D.D. (2004) Key premises, a guide to *Aedes aegypti* (Diptera: Culicidae) surveillance and control. *Bulletin of Entomological Research* 94, 201–207.

Chadee, D.D. (2010) The diel oviposition periodicity of *Aedes aegypti* (L.) (Diptera: Culicidae) in Trinidad, West Indies: effects of forced egg retention. *Bulletin of Entomological Research* 100, 599–603.

Chagas, C. (1909) Novo tripanozomiaze humana. Estudos sobre a morfolojia e o circulo evolutivo do *Schizotrypanum cruzi* n. gen., n. sp., ajenta etiologico de nova entidade morbida do homen. *Memorias do Instituto Oswaldo Cruz* 1, 159–218.

Chamberlin, T.C. (1897) The method of multiple working hypotheses. *Journal of Geology* 5, 837–848.

Chambers, R.J., Sunderland, K.D. *et al.* (1982) A survey of cereal aphids and their natural enemies in winter wheat in 1980. *Annals of Applied Biology* 101, 175–178.

Chan, W.P., Prete, F. *et al.* (1998) Visual input to the efferent control system of a fly's "gyroscope". *Science* 280, 289–292.

Chaneton, E.J. and Bonsall, M.B. (2000) Enemy-mediated apparent competition: the empirical patterns and the evidence. *Oikos* 88, 380–394.

Chapman, J.W., Reynolds, D.R. *et al.* (2002) High altitude migration of diamondback moths, *Plutella xylostella*, to the U.K., a study using radar, aerial netting, and ground trapping. *Ecological Entomology* 27, 641–650.

Chapman, J.W., Reynolds, D.R. *et al.* (2004) Migratory and foraging movements of beneficial insects: a review of radar monitoring and tracking methods. *International Journal of Pest Management* 50, 225–232.

Chapman, J.W., Reynolds, D.R. *et al.* (2015) Long-range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences. *Ecology Letters* 18, 287–302.

Chapman, R.F. (1998) *The Insects*, 4th edn. Cambridge, UK: Cambridge University Press.

Chapman, R.F. (1999) It's all in the neurones. *Entomologia Experimentalis et Applicata* 91, 259–265.

Chapman, R.F. and Joern, A. (eds) (1990) *Biology of Grasshoppers*. New York, New York, USA: Wiley.

Chapman, R.F., Page, W.W. *et al.* (1986) Bionomics of the variegated grasshopper *Zonocerus variegatus* in West and Central Africa. *Annual Review of Entomology* 31, 479–505.

Chapman, R.N. (1928) The quantitative analysis of environmental factors. *Ecology* 9, 111–122.

Chapman, R.N. (1931) *Animal Ecology, with Especial Reference to Insects*. London, UK: McGraw-Hill.

Chapuis, M.-P., Crespin., L. *et al.* (2010) Parental crowding influences life-history traits in *Locusta migratoria* females. *Bulletin of Entomological Research* 100, 9–17.

Charlesworth, D. (1985) Distribution of dioecy and self-incompatibility in angiosperms. In: Greenwood, J.J. and Slatkin, M. (eds) *Essays in Honour of John Maynard Smith*. Cambridge, UK: Cambridge University Press, pp. 237–268.

Charlesworth, D. (2000) Unlocking the secrets of self-incompatibility. *Current Biology* 10, R184–R186.

Charlesworth, D., Morgan, M.T. *et al.* (1993) Mutation accumulation in finite outbreeding and inbreeding populations. *Genetic Research* 61, 39–56.

Charnov, E.L. (1976) Optimal foraging: The marginal value theorem. *Theoretical Population Biology* 9, 129–136.

Chazdon, R.L. and Fetcher, N. (1984) Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology* 72, 553–564.

Cheke, R.A. and Holt, J. (1993) Complex dynamics of desert locust plagues. *Ecological Entomology* 18, 109–115.

Chen, P.S. (1966) Amino acid and protein metabolism in insect development. *Advances in Insect Physiology* 3, 53–132.

Chen, R.L., Sun, Y.J. *et al.* (1995) Migration of the oriental armyworm *Mythimna seperata* in East Asia in relation to weather and climate. In Drake, V.A. and Gatehouse, A.G. (eds) *Insect Migration: Tracking Resources Through Space and Time*. Cambridge, UK: Cambridge University Press.

Cheng, L. (1970) Timing of attack by *Lypha dubia* Fall. (Diptera: Tachinidae) on the winter moth, *Operophtera brumata* (L.) (Lepidoptera: Geometridae) as a factor affecting parasite success. *Journal of Animal Ecology* 39, 313–320.

Cherrill, A. (2002) Relationships between oviposition date, hatch date, and offspring size in the grasshopper *Chorthippus brunneus*. *Ecological Entomology* 27, 521–528.

Chesson, J. and Murdoch, W.W. (1986) Aggregation of risk in host-parasite models. *The American Naturalist* 127, 696–715.

Chiang, H.C. (1973) Bionomics of the northern and western corn rootworms. *Annual Review of Entomology* 18, 47–72.

Chitty, D. (1960) Population processes in the vole and their relevance to general theory. *Canadian Journal of Zoology* 38, 99–113.

Chitty, D. (1967) The natural selection of self-regulatory behavior in animal populations. *Proceedings of the Ecological Society of Australia* 2, 51–78.

Chmielewski, M.W., Khatchikian, C. *et al.* (2010) Estimating the per capita rate of population change: how well do life-history surrogates perform? *Annals of the Entomological Society of America* 103, 734–741.

Choudhury, D. (1985) Aphid honeydew: a re-appraisal of Owen and Wiegert's hypothesis. *Oikos* 45, 287–290.

Chown, S.L. and Gaston, K.J. (2000) Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology and Evolution* 15, 311–315.

Christophers, S.R. (1960) Aedes aegypti (L.) *the Yellow Fever Mosquito*; *its Life History, Bionomics and Structure*. Cambridge, UK: Cambridge University Press.

Chrystal, R.N. (1928) The *Sirex* wood-wasps and their importance in forestry. *Bulletin of Entomological Research* 19, 219–247.

Claridge, M.F., Dawah, H.A. *et al.* (1997) *Species: the Units of Biodiversity*. London, UK: Chapman and Hall.

Clark, K.E., Hartley, S.E. *et al.* (2011) Does mother know best? The preference-performance hypothesis and parent-offspring conflict in aboveground-belowground herbivore life cycles. *Ecological Entomology* 36, 117–124.

Clark, K.E., Hartley, S.E. *et al.* (2012) Investigating preference-performance relationships in aboveground-belowground life cycles: a laboratory and field study with the vine weevil (*Otiorhynchus sulcatus*). *Bulletin of Entomological Research* 102, 63–70.

Clark, L.R. (1947) An ecological study of the Australian plague locust *Chortoicetes terminifera* Walk. in the Bogan-Macquarie outbreak area of N.S.W. Bulletin of the Council for Scientific and Industrial Research Australia No. 226.

Clark, L.R. (1964) The population dynamics of *Cardiaspina albitextura* (Psyllidae). *Australian Journal of Zoology* 12, 362–380.

Clark, L.R. and Dallwitz, M.J. (1975) The life system of *Cardiaspina albitextura* (Psyllidae), 1950–1974. *Australian Journal of Zoology* 23, 523–561.

Clark, L.R., Geier, P.W. *et al.* (1967) *The Ecology of Insect Population in Theory and Practice*. London, UK: Methuen.

Clark, W.C. (1976) The environment and the genotype in polymorphism. *Zoological Journal of the Linnean Society* 58, 255–262.

Clarke, C. (1984) Upsets in the sex-ratio of some Lepidoptera. In: Vane-Wright, R.I. and Ackery, P.R. (eds) *The Biology of Butterflies*. Symposium of the Royal Entomological Society of London, No. 11. London, UK: Academic Press, pp. 255–258.

Clarke, P.A. and Garraway, E. (1994) Development of nests and composition of colonies of *Nasutitermes nigriceps* (Isoptera: Termitidae) in the mangroves of Jamaica. *Florida Entomologist* 77, 272–280.

Clausen, C.P. (1940) *Entomophagous Insects*. New York, New York, USA: McGraw-Hill.

Clausen, C.P. (1978) *Introduced Parasites and Predators of Arthropod Pests and Weeds: a World Review*. Washington, DC, USA: USDA Handbook No. 480.

Clay, K. (1990) Fungal endophytes of grasses. *Annual Review of Ecology and Systematics* 21, 275–297.

Clements, A.N. (1992/1999) *The Biology of Mosquitoes*, vols 1 and 2. Wallingford, UK: CAB International.

Clements, F.E. and Shelford, V.E. (1939) *Bio-Ecology*. New York, New York, USA: Wiley.

Coaker, T.H. and Wright, D.W. (1963) The influence of temperature on the emergence of the cabbage root fly *Erioischia brassicae* (Bouché) from overwintering pupae. *Annals of Applied Biology* 52, 337–343.

Cochrane, J. and Thornhill, W.A. (1987) Variation in annual and regional damage to sugar beet by pygmy beetles (*Atomaria linearis*). *Annals of Applied Biology* 110, 231–238.

Cockfield, D. (1988) Relative availability of nitrogen in host plants of invertebrate herbivores: three possible nutritional and physiological definitions. *Oecologia* 77, 91–94.

Codella, S.G. and Raffa, K.F. (2002) Desiccation of *Pinus* foliage induced by sawfly oviposition: effect on egg viability. *Ecological Entomology* 27, 618–621.

Coe, R.L., Freeman, P. *et al.* (1950) *Handbooks for the Identification of British Insects*. 9 (1). London, UK: Royal Entomological Society of London.

Coetzee, J.A., Byrne, M.J. *et al.* (2007) Predicting the distribution of *Eccritotarsus catarinensis*, a natural enemy of water hyacinth in South Africa. *Entomologia Experimentalis et Applicata* 125, 237–247.

Coetzee, M. (1989) Comparative morphology and multivariate analysis for the discrimination of four members of the *Anopheles gambiae* group in southern Africa. *Mosquito Systematics* 21, 100–116.

Cohen, J. (1969) Natural primate groups and a stochastic population model. *The American Naturalist* 103, 455–477.

Cohen, J.E. (1971) Mathematics as a metaphor. *Science* 172, 674–675.

Cole, L.C. (1949) The measurement of interspecific association. *Ecology* 30, 411–424.

Cole, L.C. (1954) The population consequences of life history phenomena. *The Quarterly Review of Biology* 29, 103–137.

Cole, L.C. (1958) Population fluctuations. *Proceedings of the 10th International Congress of Entomology* 2, 639–647.

Cole, L.C. (1960) Competitive exclusion. *Science* 132, 348–349; 1675–1676.

Colinvaux, P.A. (1986) *Ecology*. New York, New York, USA: Wiley.

Collett, T.S (1996) Insect navigation *en route* to the goal: multiple strategies for the use of landmarks. *The Journal of Experimental Biology* 199, 227–235.

Collins, F.H. and Paskewitz, S.M. (1995) Malaria: current and future prospects for control. *Annual Review of Entomology* 40, 195–219.

Collins, F.H., Sakai, R.K. *et al.* (1986) Genetic selection of a *Plasmodium*-refractory strain of the malaria vector *Anopheles gambiae*. *Science* 234, 607–610.

Coluzzi, M., Sabatini, A. *et al.* (2002) A polytene chromosome analysis of the *Anopheles gambiae* species complex. *Science* 298, 1416–1418.

Colwell, R.K. (1981) Group selection is implicated in the evolution of female-biased sex ratios. *Nature* 290, 401–404.

Colwell, R.K., Brehm, G. *et al.* (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322, 258–261.

Colyer, C.N. and Hammond, C.O. (1951) *Flies of the British Isles*. London, UK: Warne.

Colyvan, M. and Ginzburg, L.R. (2003) Laws of nature and laws of ecology. *Oikos* 101, 649–653.

Comins, H.N. and Noble, I.R. (1985) Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. *The American Naturalist* 126, 706–723.

Comins, H.N., Hamilton, W.D. *et al.* (1980) Evolutionary stable dispersal strategies. *Journal of Theoretical Biology* 82, 205–230.

Comins, H.N., Hassell, M.P. *et al.* (1992) The spatial dynamics of host-parasitoid systems. *Journal of Animal Ecology* 61, 735–748.

Comstock, J.H. (1940) *An Introduction to Entomology*, 9th edn. Ithaca, New York, USA: Comstock.

Condit, R., Pitman, N. *et al.* (2002) Beta-diversity in tropical forest trees. *Science* 295, 666–669.

Connell, J.H. (1980) Diversity and the coevolution of competitors; or, the ghost of competition past. *Oikos* 35, 131–138.

Connell, J.H. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* 122, 661–696.

Conner, J.K. (2003) Artificial selection: a powerful tool for ecologists. *Ecology* 84, 1650–1660.

Connor, E.F. and Taverner, M.P. (1997) The evolution and adaptive significance of the leaf-mining habit. *Oikos* 79, 6–25.

Conte, A., Gilbert, M. *et al.* (2009) Eight years of entomological surveillance in Italy show no evidence of *Culicoides imicola* geographical range expansion. *Journal of Applied Ecology* 46, 1332–1339.

Cook, A.G. and Perfect, T.J. (1985) Seasonal abundance of macropterous *Nilaparvata lugens* and *Sogatella furcifera* based on presumptive macroptery in fifth instar nymphs. *Ecological Entomology* 10, 249–258.

Cook, A.G. and Perfect, T.J. (1989) The population characteristics of the brown planthopper, *Nilaparvata lugens*, in the Philippines. *Ecological Entomology* 14, 1–9.

Cook, L.M., Thomason, E.W. *et al.* (1976) Population structure, dynamics and dispersal of the tropical butterfly *Heliconius charitonius*. *Journal of Animal Ecology* 45, 851–863.

Cook, S.E., Vernon, J.G. *et al.* (1994) Mate choice in the polymorphic African swallowtail butterfly, *Papilio dardanus*: male-like females may avoid sexual harassment. *Animal Behaviour* 47, 389–397.

Cook, S.M., Khan, Z.R. *et al.* (2007) The use of push-pull strategies in integrated pest management. *Annual Review of Entomology* 52, 375–400.

Cook, W.C. (1924) The distribution of the pale western cutworm (*Porosagrotis orthogonia* Morr.): a study in physical ecology. *Ecology* 5, 60–69.

Cook, W.C. (1925) The distribution of the alfalfa weevil (*Phytonomus posticus*, Gyll.). A study in physical ecology. *Journal of Agricultural Research* 30, 479–491.

Cooley, J.R., Simon, C. *et al.* (2001) Allochronic speciation, secondary contact, and reproductive character displacement in periodical cicadas (Hemiptera: *Magicicada* chk spp.): genetic, morphological and behavioural evidence. *Molecular Ecology* 10, 661–671.

Coope, G.R. (1977) Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (last) cold stage. *Philosophical Transactions of the Royal Society B* 280, 313–340.

Coope, G.R. (1979) Late Cenozoic fossil Coleoptera: evolution, biogeography, and ecology. *Annual Review of Ecology and Systematics* 10, 247–267.

Cooper-Driver, G.A. (1978) Insect-fern associations. *Entomologia Experimentalis et Applicata* 24, 310–316.

Cooperband, M.F. and Vinson, S.B. (2002) Host-acceptance requirements of *Melittobia digitata* (Hymenoptera: Eulophidae), a parasitoid of mud dauber wasps. *Biological Control* 17, 23–28.

Copleston, F. (1957) *A History of Philosophy*, vol. 2. Westminster, Massachusetts, USA: Newman Press.

Copping, L.G. (ed.) (2004) *The Manual of Biocontrol Agents*. Alton, UK: BCPC Publications.

Corbet, P.S. (1952) An adult population study of *Pyrrhosoma nymphula* Sulzer. (Odonata: Coenagrionidae). *Journal of Animal Ecology* 21, 206–222.

Corbet, P.S. (1964) Temporal patterns or emergence in aquatic insects. *The Canadian Entomologist* 96, 264–279.

Corbet, P.S. (1999) *Dragonflies: Behaviour and Ecology*. Colchester, UK: Harley Books.

Corbet, S.A. and Huang, S-Q. (2016) Small bees overheat in sunlit flowers: do they make cooling flights? *Ecological Entomology* 41, 344–350.

Cordero, A. (1992) Density-dependent mating success and colour polymorphism in females of the damselfly *Ischnura graellsii* (Odonata: Coenagrionidae). *Journal of Animal Ecology* 61, 769–780.

Corlay, F. and Boivin, G. (2008) Seasonal development of an invasive exotic species, *Contarinia nasturtii* (Diptera: Cecidomyiidae), in Quebec. *Environmental Entomology* 37, 907–913.

Corley, J.C., Villacide, J.M. *et al.* (2007) Spatial dynamics of a *Sirex noctilio* wood wasp population within a pine plantation in Patagonia, Argentina. *Entomologia Experimentalis et Applicata* 125, 231–236.

Cornell, H.V. and Hawkins, B.A. (1995) Survival patterns and mortality sources of herbivorous insects - some demographic trends. *The American Naturalist* 145, 563–593.

Cornell, H.V. and Lawton, J.H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities:

a theoretical perspective. *Journal of Animal Ecology* 61, 1–12.

Corning, P.A. (2014) Evolution "on purpose": how behaviour has shaped the evolutionary process. *Biological Journal of the Linnean Society* 112, 242–260.

Corrie, A.M., Crozier, R.H. *et al.* (2002) Clonal reproduction and population genetic structure of grape phylloxera, *Daktulosphaira vitifoliae*, in Australia. *Heredity* 88, 203–211.

Costa, J.T. (2013) Hamiltonian inclusive fitness: a fitter fitness concept. *Biology Letters* 9, 20130335.

Cott, H.B. (1940) *Adaptive Coloration in Animals*. London, UK: Methuen.

Coulson, J.C. (1959) Observations on the Tipulidae (Diptera) of the Moor House Nature Reserve. *Transactions of the Royal Entomological Society of London* 111, 157–174.

Coulson, R.N. (1979) Population dynamics of bark beetles. *Annual Review of Entomology* 24, 417–447.

Coulson, R.N., Mayyasi, A.M. *et al.* (1976) Interspecific competition between *Monochamus titillator* and *Dendroctonus frontalis*. *Environmental Entomology* 5, 235–247.

Coulson, S.J. and Bale, J.S. (1990) Characterization and limitation of rapid cold hardening in the house fly *Musca domestica*. *Journal of Insect Physiology* 36, 207–211.

Coupland, J.B. (1991) Oviposition response of *Simulium reptans* (Diptera: Simuliidae) to the presence of conspecific eggs. *Ecological Entomology* 16, 11–15.

Courtney, S.P. (1984) The evolution of egg clustering by butterflies and other insects. *The American Naturalist* 123, 276–281.

Courtney, S.P. and Duggan, A.E. (1983) The population biology of the orange tip butterfly *Anthocharis cardamines* in Britain. *Ecological Entomology* 8, 271–281.

Cowley, M.J.R., Thomas, C.D. *et al.* (2001) Density-distribution relationships in British butterflies. 1. The effect of mobility and spatial scale. *Journal of Animal Ecology* 70, 410–425.

Cox, F.E.G. (2002) History of human parasitology. *Clinical Microbiology Reviews* 15, 595–612.

Cox, P.A. (1991) Abiotic pollination: an evolutionary escape for animal-pollinated angiosperms. *Transactions of the Royal Society B* 333, 217–224.

Coyle, D.R., Nebeker, T.E. *et al.* (2005) Biology and management of insect pests in North American intensively managed hardwood forest systems. *Annual Review of Entomology* 50, 1–29.

Coyle, D.R., Duman, J.G. *et al.* (2011) Temporal and species variation in cold hardiness among invasive rhyzophagous weevils (Coleoptera: Curculionidae) in a northern hardwood forest. *Annals of the Entomological Society of America* 104, 59–67.

Coyne, J.A. (1985) Genetic studies on three sibling species of *Drosophila* with relationship to theories of speciation. *Genetical Research* 46, 169–192.

Coyne, J.A. (1992) Genetics and speciation. *Nature* 355, 511–515.

Coyne, J.A. and Orr, H.A. (1998) The evolutionary genetics of speciation. *Philosophical Transactions of the Royal Society of London B* 353, 287–305.

Coyne, J.A. and Orr, H.A. (2004) *Speciation*. Sunderland, Massachusetts, USA: Sinauer.

Coyne, J.A., Boussy, I.A. *et al.* (1982) Long-distance migration of *Drosophila*. *The American Naturalist* 119, 589–595.

Coyne, J.A., Barton, N.H. *et al.* (2000) Is Wright's shifting balance process important in evolution? *Evolution* 54, 306–317.

Cozzolino, S. and Widmer, A. (2005) Orchid diversity: an evolutionary consequence of deception. *Trends in Ecology and Evolution* 20, 487–494.

Craig, G.B. (1967) Mosquitoes: female monogamy induced by male accessory gland substances. *Science* 156, 1499–1501.

Craig, T.P., Itami, J.K. *et al.* (1990) Intraspecific competition and facilitation by a shoot-galling sawfly. *Journal of Animal Ecology* 59, 147–159.

Craig, W. (1918) Appetites and aversions as constituents of instinct. *Biological Bulletin* 34, 91–107.

Cranston, P.S. (2016) Madagascan "wild" silk. *Antenna* 40, 114–118.

Cranston, P.S. (2018) "Pamageddon" revisited. *Antenna* 42, 14–17.

Crawley, M.J. (1989) Insect herbivores and plant population dynamics. *Annual Review of Entomology* 34, 531–564.

Crawley, M.J. (1997) (ed.) *Plant Ecology*. Oxford, UK: Blackwell Science.

Crawley, M.J. and Akhteruzzaman, M. (1988) Individual variation in the phenology of oak trees and its consequences for herbivorous insects. *Functional Ecology* 2, 409–415.

Crawley, M.J. and Nachapong, M. (1984) Facultative defences and specialist herbivores? Cinnabar moth (*Tyria jacobaeae*) on the regrowth foliage of ragwort (*Senicio jacobaea*). *Ecological Entomology* 9, 389–393.

Crawley, M.J. and Pattrasudhi, R. (1988) Interspecific competition between insect herbivores: asymmetric competition between the cinnabar moth and the ragwort seed-head fly. *Ecological Entomology* 13, 243–249.

Creaser, A., Pateman, J.E. *et al*. (2008) A surfeit of female *Pieris rapae* butterflies in New Zealand: a string of coincidences or something more sinister? *Antenna* 32, 199–204.

Critchley, B.R. (1973) Parasitism of the larvae of some Carabidae (Coleoptera). *Journal of Entomology A* 48, 37–42.

Croft, B.A. and Jeppson, L.R. (1970) Comparative studies on four strains of *Typhlodromus occidentalis*. 2. Laboratory toxicity to ten compounds common to apple pest control. *Journal of Economic Entomology* 63, 845–850.

Croft, B.A. and Hoyt, S.C. (eds) (1983) *Integrated Pest Management of Insect Pests of Pome and Stone Fruits*. New York, New York, USA: Wiley.

Crombie, A.C. (1947) Interspecific competition. *Journal of Animal Ecology* 16, 44–73.

Cronin, J.T. and Reeve, J.D. (2005) Host-parasitoid spatial ecology: a plea for landscape-level synthesis. *Proceedings of the Royal Society B* 272, 2225–2235.

Cronin, J.T. and Strong, D.R. (1993) Substantially submaximal oviposition rates by a mymarid egg parasitoid in the laboratory and field. *Ecology* 74, 1813–1825.

Cronquist, A. (1988) *The Evolution and Classification of Flowering Plants*, 2nd edn. New York, New York, USA: The New York Botanical Garden.

Crosskey, R.W. (1990) *The Natural History of Blackflies*. Chichester, UK: Wiley.

Crow, J.F. and Kimura, M. (1970) *An Introduction to Population Genetics Theory*. New York, New York, USA: Harper and Row.

Crowley, T.J. (2000) Causes of climate change over the past 1000 years. *Science* 289, 270–277.

Crozier, L. (2004) Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology* 85, 231–241.

Cui, F., Qiao, C.-L. *et al*. (2007) Genetic differentiation of *Culex pipiens* (Diptera: Culicidae) in China. *Bulletin of Entomological Research* 97, 291–297.

Currie, R.C., Wong, B. *et al*. (2003) Ancient tripartite coevolution in the attine ant-microbe symbiosis. *Science* 299, 386–388.

Curtis, C.F. (1976) Population replacement in Culex fatigans by means of cytoplasmic incompatibility. *Bulletin of the World Health Organization* 53, 107–119.

Curtis, C.F. (1992) Making mosquitoes harmless. *Parasitology Today* 8, 305.

Curtis, C.F., Grover, K. *et al*. (1976) Comparative field cage tests of the population suppressing efficiency of three genetic control systems for *Aedes aegypti*. *Heredity* 36, 11–29.

Curtis, J. (1860) *Farm Insects: Being the Natural History and Economy of the Insects Injurious to the Field Crops of Great Britain and Ireland*. Glasgow: Blackie and Son.

Cuthbertson, A.G.S. (2015) *Bemisia tabaci*: preventing a global pest from establishing in the UK. *Antenna* (Special Edition, 2015), 87–88.

Cuthbertson, A.G.S., Walters, K.F.A. *et al*. (2007) Efficacy of the entomopathogenic nematode, *Steinernema feltiae*, against sweet potato whitefly *Bemisia tabaci* (Homoptera: Aleyrodidae) under laboratory and glasshouse conditions. *Bulletin of Entomological Research* 97, 9–14.

Cyr, H. (1997) Does inter-annual variability in population density increase with time? *Oikos* 79, 549–558.

Daane, K.M. and Johnson, M.W. (2010) Olive fruit fly: managing an ancient pest in modern times. *Annual Review of Entomology* 55, 151–169.

Daane, K.M., Wang, X. *et al*. (2015) Classical biological control of olive fruit fly in California, USA: release and recovery of introduced parasitoids. *BioControl* 60, 317–333.

D'Abrera, B. (1981) *Butterflies of the Neotropical Region*. Melbourne, Australia: Landsdowne.

D'Abrera, B. (1986) *Sphingidae Mundi: Hawk Moths of the World*. Faringdon, UK: E.W. Classey.

Dafni, A. (1984) Mimicry and deception in pollination. *Annual Review of Ecology and Systematics* 15, 259–278.

Dale, C. and Moran, N.A. (2006) Molecular interactions between bacterial symbionts and their hosts. *Cell* 126, 453–465.

D'Alessandro, M., Held, M. *et al.* (2006) The role of indole and other shikimic acid derived maize volatiles in the attraction of two parasitic wasps. *Journal of Chemical Ecology* 32, 2733–2748.

Dalthorp, D. and Dreves, A.J. (2008) Spatio-temporal ecology and management of cabbage maggots. *Environmental Entomology* 37, 409–418.

Daly, H.V., Doyen, J.T. *et al.* (1998) *Introduction to Insect Biology and Diversity*, 2nd edn. Oxford, UK: Oxford University Press.

Damon, A. (2000) A review of the biology and control of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Bulletin of Entomological Research* 90, 453–465.

Danks, H.V. (1971a) Populations and nesting sites of some aculeate Hymenoptera nesting in *Rubus*. *Journal of Animal Ecology* 40, 63–77.

Danks, H.V. (1971b) Nest mortality factors in stem-nesting aculeate Hymenoptera. *Journal of Animal Ecology* 40, 79–82.

Danks, H.V. (1978) Modes of seasonal adaptation in the insects. (1) Winter survival. *The Canadian Entomologist* 110, 1167–1205.

Danks, H.V. (2002) Modification of adverse conditions by insects. *Oikos* 99, 10–24.

Danks, H.V. (2006) Short life cycles in insects and mites. *The Canadian Entomologist* 138, 407–463.

Danks, H.V. (2007) The elements of seasonal adaptations in insects. *The Canadian Entomologist* 139, 1–44.

Danthanarayana, W. (1983) Population ecology of the light brown apple moth, *Epiphyas postvittana* (Lepidoptera; Tortricidae). *Journal of Animal Ecology* 52, 1–33.

Danyk, T., Mackauer, M. *et al.* (2005a) Reduced food consumption in the grasshopper *Melanoplus sanguinipes* (Orthoptera: Acrididae) parasitised by *Blaesoxipha atlanis* (Diptera: Sarcophagidae). *The Canadian Entomologist* 137, 356–366.

Danyk, T., Mackauer, M. *et al.* (2005b) The influence of host suitability on the range of grasshopper species utilised by *Blaesoxipha atlanis* (Diptera: Sarcophagidae) in the field. *Bulletin of Entomological Research* 95, 571–578.

Darnell, R.M. (1961) Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. *Ecology* 42, 553–568.

Darwin, C.R. (1859) *On the Origin of Species by Means of Natural Selection*. London, UK: John Murray.

Darwin, C.R. (1862) *On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects*. London, UK: John Murray.

Darwin, C.R. (1871) *The Descent of Man and Selection in Relation to Sex*. London, UK: John Murray.

Darwin, E. (1794/1796) *Zoonomia, or, The Laws of Organic Life,* vols 1 and 2. London, UK: J. Johnson.

Darwin, E. (1800) *Phytologia: or the Philosophy of Agriculture and Gardening*. London, UK: J. Johnson.

Davidson, J. and Andrewartha, H.G. (1948) Annual trends in a natural population of *Thrips imaginis* (Thysanoptera). *Journal of Animal Ecology* 17, 193–199.

Davidson, R.H. and Lyon, W.F. (1986) *Insect Pests of Farm, Garden and Orchard*, 8th edn. New York, New York, USA: Wiley.

Davis, M.A. (1984) The flight and migration ecology of the red milkweed beetle (*Tetraopes tetraophthalmus). Ecology* 65, 230–234.

Davis, N.K. and Jones, P.E. (1986) Insects on isolated colonies of common rock-rose *Helianthemum chamaecistus*. *Ecological Entomology* 11, 267–281.

Dawkins, R. (1982) *The Extended Phenotype*. Oxford, UK: Oxford University Press.

Dawkins, R. (1989) *The Selfish Gene*, 2nd edn. Oxford, UK: Oxford University Press.

Day, K. (1984) Phenology, polymorphism and insect-plant relationships of the larch bud-moth, *Zeiraphera diniana* (Guenée) (Lepidoptera: Tortricidae), on alternative hosts in Britain. *Bulletin of Entomological Research* 74, 47–64.

de Bach, P. (1943) The importance of host-feeding by adult parasites in the reduction of host populations. *Journal of Economic Entomology* 36, 647–658.

de Bach, P. (1974) *Biological Control by Natural Enemies*. Cambridge, UK: Cambridge University Press.

De Bach, P. and Rosen, D. (1991*) Biological Control by Natural Enemies*. Cambridge, UK: Cambridge University Press.

De Block, M. and Stoks, R. (2007) Flight-related body morphology shapes mating success in a damselfly. *Animal Behaviour* 74, 1093–1098.

De Block, M., Campero, M. *et al.* (2008) Developmental costs of rapid growth in a damselfly. *Ecological Entomology* 33, 313–318.

Deevey, E.S. (1947) Life tables for natural populations of animals. *The Quarterly Review of Biology* 22, 283–314.

Deevey, G.B. and Deevey, E.S. (1945) A life table for the black widow. *Transactions of the Connecticut Academy of Arts and Sciences* 36, 115–134.

Degefu, D.T., Hurley, B.P. *et al.* (2013) Parallel host range expansion in two unrelated cossid moths infesting *Eucalyptus nitens* on two continents. *Ecological Entomology* 38, 112–116.

De Graaf, J., Govender, P. *et al.* (2005) Efficacy of pseudostem and pheromone seasonal trapping of the banana weevil *Cosmopolites sordidus* in South Africa. *International Journal of Pest Management* 51, 209–218.

De Jong, G. (1979) The influence of the distribution of juveniles over patches of food on the dynamics of a population. *Netherlands Journal of Zoology* 29, 33–51.

Dekker, T., Geier, M. *et al.* (2005) Carbon dioxide instantly sensitises female yellow fever mosquitoes to human skin odours. *The Journal of Experimental Biology* 208, 2963–2972.

Del Bianco Faria, L., Orsi, L. *et al.* (1999) Larval predation by *Chrysomya albiceps* on *Cochliomyia macellaria*, *Chrysomya megacephala* and *Chrysomya putoria*. *Entomologia Experimentalis et Applicata* 90, 149–155.

Del Genio, A.D. (2002) The dust settles on water vapor feedback. *Science* 296, 665–666.

Dempster, J.P. (1961) The analysis of data obtained by regular sampling of an insect population. *Journal of Animal Ecology* 30, 429–432.

Dempster, J.P. (1975) *Animal Population Ecology*. New York, New York, USA: Academic Press.

Dempster, J.P. (1982) The ecology of the cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera, Arctiidae). *Advances in Ecological Research* 12, 1–36.

Dempster, J.P. (1983) Natural control of populations of butterflies and moths. *Biological Reviews* 58, 461–481.

Dempster, J.P. (1992) Evidence of an oviposition-deterring pheromone in the orange-tip butterfly, *Anthocharis cardamines* (L.). *Ecological Entomology* 17, 83–85.

Dempster, J.P. and McLean, I.F.G. (eds) (1998) *Insect Populations in Theory and Practice*. Dordrecht, Germany: Kluwer Academic Publishers, pp. 417–422.

Dempster, J.P. and Pollard, E. (1981) Fluctuations in resource availability and insect populations. *Oecologia* 50, 412–416.

Dempster, J.P. and Pollard, E. (1986) Spatial heterogeneity, stochasticity and the detection of density dependence in animal populations. *Oikos* 46, 413–416.

Dempster, J.P., King, M.L. *et al.* (1976) The status of the swallowtail butterfly in Britain. *Ecological Entomology* 1, 71–84.

Den Bieman, C.F.M. (1988) Co-existence of pseudogamous and sexual plant-hoppers of the genus *Ribautodelphax* (Homoptera: Delphacidae). *Ecological Entomology* 13, 383–390.

den Boer, P.J. (1968) Spreading of risk and stabilisation of animal numbers. *Acta Biotheoretica* 18, 165–194.

den Boer, P.J. (1977) Dispersal power and survival. Carabids in cultivated countryside. *Miscellaneous Papers* 14, 1–190.

den Boer, P.J. (1982) On the stability of animal populations, or how to survive in a heterogeneous and changeable world. In: Mossakowski, D. and Roth, G. (eds), *Environmental Adaptation* and *Evolution*. Stuttgart, Germany: Gustav Fischer.

den Boer, P.J. (1985) Fluctuations of density and survival of carabid populations. *Oecologia* 67, 322–330.

den Boer, P.J. (1998) The role of density-independent processes in the stabilisation of insect populations. In: Dempster, J.P. and McLean, I.F.G. (eds) (1998) *Insect Populations in Theory and Practice*. Dordrecht, The Netherlands: Kluwer Academic Publishers, pp. 53–80.

den Boer, P.J. and Reddingius, J. (1996*) Regulation and Stabilisation Paradigms in Population Ecology*. London, UK: Chapman and Hall.

den Boer, P.J. and Sanders, G. (1970) Structure of vegetation and microweather. Miscellaneous Papers Landbouwhogeschool, *Wageningen* 6, 33–53.

den Boer, P.J., Luff, M.L. *et al.* (1986) *Carabid Beetles. Their Adaptations and Dynamics*. Stuttgart, Germany: Gustav Fischer.

Denison, R.F. *et al.* (2003) Darwinian agriculture. *The Quarterly Review of Biology* 78, 145–168.

Denlinger, D.L. and Lee, R.E. (2010) *Low Temperature Biology of Insects*. Cambridge, UK: Cambridge University Press.

Denno, R.F. and Benrey, B. (1997) Aggregation facilitates larval growth in the Neotropical nymphalid butterfly *Chlosyne janais*. *Ecological Entomology* 22, 133–141.

Denno, R.F. and Perfect, T.J. (eds) (1994) *Planthoppers: Their Ecology and Management*. New York, USA: Chapman and Hall.

Denno, R.F. and Roderick, G.K. (1990) Population biology of plant-hoppers. *Annual Review of Entomology* 35, 489–520.

Denno, R.F., McClure, M.S. *et al.* (1995) Interspecific interactions in phytophagous insects. *Annual Review of Entomology* 40, 297–331.

Dent, D. (2000) *Insect Pest Management*, 2nd edn. Wallingford, UK: CAB International.

Dernisky, A.K., Evans, R.C. *et al.* (2005) Characterization of early floral damage by cranberry tipworm (*Dasineura oxycoccana* Johnson) as a precursor to reduced fruit set in rabbiteye blueberry (*Vaccinium ashei* Reade). *International Journal of Pest Management* 51, 143–148.

De Ruiter, L. (1956) Countershading in caterpillars. An analysis of its adaptive significance. *Archivas Neerlanddaises de Zoologie* 11, 285–341.

Descimon, H. (2006) La conservation des *Parnassius* de France. Situation en 1995 et situation en 2006, 11 ans après. *Bulletin des Lépidoptéristes Parisiens* 15, 34–55.

Desjeux, P. and Alvar, J. (2003) Leishmania/HIV co-infections: epidemiology in Europe. *Annals of Tropical Medicine and Parasitology* 97 (Suppl.1), 3–15.

Desmond, A. (1994) *Huxley*. London, UK: Michael Joseph.

Desouhant, E., Driessen, G. *et al.* (2003) Dispersal between host populations in field conditions: navigation rules in the parasitoid *Venturia canescens*. *Ecological Entomology* 28, 257–267.

De Souza, A.P., Gaspar, M. *et al.* (2008) Elevated CO2 increases photosynthesis, biomass and productivity, and modifies gene expression in sugarcane. *Plant Cell and Environment* 31, 1116–1127.

Dethier, V.G. (1954) Evolution of feeding preferences in phytophagous insects. *Evolution* 8, 33–54.

Dethier, V.G. (1961) Behavioural aspects of protein ingestion by the blowfly *Phormia regina* Meigen. *Biological Bulletin* 121, 456–470.

Dethier, V.G. (1980) Evolution of receptor sensitivity to secondary plant substances with special reference to deterrents. *The American Naturalist* 115, 45–66.

Dethier, V.G. and Bodenstein, D. (1958) Hunger in the blowfly. *Zeitschrift für Tierpsychologie* 15, 129–140.

Dettner, K. and Liepert, C. (1994) Chemical mimicry and camouflage. *Annual Review of Entomology* 39, 129–154.

Devignat, R. (1951) Varietes del espèce *Pasturella pestis*. Nouvelle hypothèse. *Bulletin of the World Health Organisation* 4, 242–263.

DeVries, P.J. (1979) Occurrence of fly maggots in adult *Morpho theseus* (Lep.: Morphinae) females from Costa Rica. *Brenesia* 16, 223.

DeVries, P.J. (1984) Butterflies and Tachinidae: does the parasite always kill its host? *Journal of Natural History* 18, 323–326.

Diamond, J.M. (1999) *Guns, Germs, and Steel*. London, UK: Norton.

Dias, P.C. (1996) Sources and sinks in population biology. *Trends in Ecology and Evolution* 11, 326–330.

Dice, L.R. (1952) *Natural Communities*. Ann Arbor, Michigan, USA: University of Michigan Press.

Dicke, M. and Grostal, P. (2001) Chemical detection of natural enemies by arthropods: an ecological perspective. *Annual Review of Ecology and Systematics* 32, 1–23.

Dillon, R.J. and Dillon, V.M. (2004) The gut bacteria of insects: non-pathogenic interactions. *Annual Review of Entomology* 49, 71–92.

Dingle, H. (1968) The influence of environment and heredity on the flight activity of the milkweed bug, *Oncopeltus*. *The Journal of Experimental Biology* 48, 175–184.

Dingle, H. (1972) Migration strategies of insects. *Science* 175, 1327–1335.

Dingle, H. (1996) Heritability of wing length in nature for the milkweed bug, *Oncopeltus fasciatus*. *Evolution* 50, 442.

Dingle, H. (2001) The evolution of migratory syndromes in insects. In: Woiwod, I.P., Reynolds, D. R. *et al.* (eds). *Insect Movement: Mechanisms and Consequences*. Wallingford, UK: CAB International, pp. 159–181.

Disney, R.H.L. (1994) *Scuttle Flies: The Phoridae*. London, UK: Chapman and Hall.

Dixon, A.F.G. (1998) *Aphid Ecology*, 2nd edn. London, UK: Chapman and Hall.

Dixon, A.F.G. (2000) *Insect-Predator-Prey Dynamics: Ladybird Beetles and Biological*

Control. Cambridge, UK: Cambridge University Press.

Dixon, A.G.F. and Agarwala, B.K. (2002) Triangular fecundity function and ageing in ladybird beetles. *Ecological Entomology* 27, 433–440.

Dixon, A.G.F., Kindlmann, P. *et al.* (1987) Why so few species of aphids, especially in the tropics? *The American Naturalist* 129, 580–592.

Dixon, A.G.F., Honěk, A. *et al.* (2009) Relationship between the maximum and minimum thresholds for development in insects. *Functional Ecology* 23, 257–264.

Dixon, J. E. (2008) Aspects of Polymorphism in the Grasshopper *Orphulella punctata* (DeGeer) *in Jamaica*. Unpublished thesis of the University of the West Indies.

Doane, C.C. (1970) Primary pathogens and their role in the development of an epizootic in the gypsy moth. *Journal of Invertebrate Pathology* 15, 21–33.

Dobzhansky, T. (1937) *Genetics and the Origin of Species*. New York, New York, USA: Columbia University Press.

Dobzhansky, T. (1940) Speciation as a stage in evolutionary divergence. *The American Naturalist* 74, 312–321.

Dobzhansky, T. (1943) Genetics of natural populations 1X. Temporal changes in the composition of populations of *Drosophila pseudoobscura*. *Genetics* 28, 142–160.

Dobzhansky, T. (1950) Evolution in the tropics. *American Scientist* 38, 209–221.

Dobzhansky, T. (1959) Blyth, Darwin, and natural selection. *The American Naturalist* 93, 204–206.

Dobzhansky, T. (1970) *Genetics and the Evolutionary Process*. New York, New York, USA: Columbia University Press.

Doerr, R., Franz, K. *et al.* (1909) *Das Pappatacifieber. Ein Endemisches Dreitage-fieber im Adriactischen Kustengebiete Oesterreich-Ungarns*. Vienna, Austria: F. Denticke.

Dogramaci, M., Rondon, S.I *et al.* (2008) The effect of soil depth and exposure to winter conditions on survival of the potato tuberworm, *Phthorimaea operculella*. *Entomologia Experimentalis et Applicata* 129, 332–339.

Dollet, M. (1984) Plant diseases caused by flagellate protozoa (*Phytomonas*). *Annual Review of Phytopathology* 22, 115–132.

Dolling, W.D. (1991) *The Hemiptera*. Oxford, UK: Oxford University Press.

Döring, T.F., Archetti, M. *et al.* (2009) Autumn leaves seen through herbivore eyes. *Proceedings of the Royal Society B* 276, 121–127.

Döring, T.F., Skellern, M. *et al.* (2012) Colour choice behaviour in the pollen beetle, *Meligethes aeneus* (Coleoptera: Nitidulidae). *Physiological Entomology* 37, 360–368.

Dornhaus, A. and Chittka, L. (1999) Evolutionary origins of bee dances. *Nature* 401, 38.

Dosdall, L.M., Zalucki, M.P. *et al.* (2012) Developmental responses of the diamondback moth parasitoid *Diadegma semiclausum* (Hellén) (Hymenoptera: Ichneumonidae) to temperature and host plant species. *Bulletin of Entomological Research* 102, 373–384.

Douglas, A.E. (1998) Nutritional interactions in insect-microbial symbioses: Aphids and their symbiotic bacteria *Buchnera*. *Annual Review of Entomology* 43, 17–37.

Doury, G. and Rojas-Rousse, D. (1994) Reproductive potential in the parasitoid *Eupelmus orientalis* (Hymenoptera: Eupelmidae). *Bulletin of Entomological Research* 84, 199–206.

Doutt, R.L. (1959) The biology of parasitic Hymenoptera. *Annual Review of Entomology* 4, 161–182.

Doutt, R.L. and Nakata, J. (1973) The *Rubus* leafhopper and its egg parasitoid: an endemic biotic system useful in grape-pest management. *Environmental Entomology* 2, 381–386.

Dover, G. (1982) Molecular drive: a cohesive mode of species evolution. *Nature* 299, 111–117.

Drake, V.A. and Gatehouse, A.G. (eds) (1995) *Insect Migration: Tracking Resources Through Space and Time*. Cambridge, UK: Cambridge University Press.

Drake, V.A., Gatehouse, A.G. *et al.* (1995) Insect migration: a holistic model. In: Drake, V.A. and Gatehouse, A.G. (eds) *Insect Migration: Tracking Resources Through Space and Time*. Cambridge, UK: Cambridge University Press, pp. 427–457.

Drake, V.A., Gregg, P.C. *et al.* (2001) Characterising insect migration systems in inland Australia with novel and traditional methodologies. In: Woiwod, I.P., Reynolds, D. R. *et al.* (eds) *Insect Movement: Mechanisms and Consequences*. Wallingford, UK: CAB International, pp. 207–233.

Draper, J. (1980) The direction of desert locust migration. *Journal of Animal Ecology* 49, 959–974.

Dreisig, H. (1981) The rate of predation and its temperature dependence in a tiger beetle, *Cicindella hybrida*. *Oikos* 36, 196–202.

Dressler, R.L. (1982) Biology of the orchid bees (Euglossini). *Annual Review of Ecology and Systematics* 13, 373–394.

Drezen, J.-M., Provost, B. *et al.* (2003) Polydnavirus genome: integrated versus free virus. *Journal of Insect Physiology* 49, 407–417.

Dudley, R. (1995) Extraordinary flight performance of orchid bees. *The Journal of Experimental Biology* 198, 1065–1070.

Dudley, R. (2000) *The Biomechanics of Insect Flight*. Princeton, New Jersey, USA: Princeton University Press.

Dudley, R. (2001) The biomechanics and functional diversity of flight. In: Woiwod, I.P., Reynolds, D.R. *et al.* (eds) *Insect Movement: Mechanisms and Consequences*. Wallingford, UK: CAB International.

Duman, J.G. (2001) Antifreeze and ice nucleator proteins in terrestrial arthropods. *Annual Review of Physiology* 63, 327–357.

Duplouy, A. and Hanski, I. (2015) Small spermatophore size and reduced female fitness in an isolated butterfly population. *Ecological Entomology* 40, 167–174.

Durrett, R. and Levin, S.A. (1994) Stochastic spatial models: a user's guide to ecological applications. *Philosophical Transactions of the Royal Society of London B* 343, 329–350.

Dusenbery, D.B. (1989) Optimal search direction for an animal flying or swimming in a wind or current. *Journal of Chemical Ecology* 15, 2511–2519.

Dussourd, D.E., Ubik, K. *et al.* (1988) Biparental defensive endowment of eggs with acquired plant alkaloid in the moth Utetheisa ornatrix. *PNAS* 85, 5992–5996.

Duviard, D. (1977) Migration of *Dysdercus* spp. (Hemiptera: Pyrrhocoridae) related to movements of the Inter-Tropical Convergence Zone in W. Africa. *Bulletin of Entomological Research* 67, 185–204.

Duyck, P.-F., Dortel, E. *et al.* (2012) Effect of environment and fallow period on *Cosmopolites sordidus* population dynamics at the landscape scale. *Bulletin of Entomological Research* 102, 583–588.

Dwyer, G., Dushoff, J. *et al.* (2000) Pathogen-driven cycles in forest defoliators revisited: building models from experimental data. *The American Naturalist* 156, 105–120.

Dybas, H.S. and Davis, D.D. (1962) A population census of seventeen-year periodical cicadas (Homoptera: Cicadidae: Magicicada). *Ecology* 43, 432–444.

Dye, C. (1984) Competition amongst larval *Aedes aegypti*: the role of interference. *Ecological Entomology* 9, 355–357.

Dye, C. (1992) The analysis of parasite transmission by bloodsucking insects. *Annual Review of Entomology* 37, 1–19.

Dyer, L. A. (1995) Tasty generalists and nasty specialists? A comparative study of antipredator mechanisms in tropical lepidopteran larvae. *Ecology* 76,1483–1496.

Dyer, A.G., Rosa, M.G.P. *et al.* (2008) Honey bees can recognise images of complex natural scenes for use as potential landmarks. *The Journal of Experimental Biology* 211, 1180–1186.

Dyer, F.C. (2002) The biology of dance language. *Annual Review of Entomology* 47, 917–949.

East, R. (1974) Predation on the soil-dwelling stages of the winter moth at Wytham Woods, Berkshire. *Journal of Animal Ecology* 43, 611–626.

Eastop, V.F. (1978) Determinants of local diversity in phytophagous insects : host specialists in tropical environments. *Symposium of the Royal Entomological Society of London*, no. 9. London, UK: Academic Press.

Ebert, D., Haag, C. *et al.* (2002) A selective advantage to immigrant genes in a *Daphnia* metapopulation. *Science* 295, 485–488.

Edney, E.B. (1977) *Water Balance in Land Arthropods*. Berlin, Germany: Springer.

Edney, E.B. (1980) The components of water balance. In: Locke, M. and Smith, D.S. (eds) *Insect Biology in the Future*. New York, New York, USA: Academic Press, pp. 39–58.

Edney, E.B. and Barrass, R. (1962) The body temperature of the tsetse fly, *Glossina morsitans* Westwood (Diptera; Muscidae). *Journal of Insect Physiology* 8, 469–481.

Edson, K.M., Vinson, S.B. *et al.* (1981) Virus in a parasitoid wasp: suppression of the cellular immune response in the parasitoid's host. *Science* 211, 582–583.

Edwards, P.J. and Wratten, S.D. (1985) Induced plant defences against insect grazing: fact or artefact? *Oikos* 44, 70–74.

Eggleton, P. and Belshaw, R. (1992) Insect parasitoids: an evolutionary overview. *Philosophical Transactions of the Royal Society B* 337, 1–20.

Ehler, L.E. and Bottrell, D.G. (2000) The illusion of integrated pest management. *Issues in Science and Technology* 16, 61–64.

Ehrlich, P.R. and Raven, P.H. (1964) Butterflies and plants: a study in coevolution. *Evolution* 18, 586–608.

Ehrlich, P.R. and Raven, P.H. (1969) Differentiation of populations. *Science* 165, 1228–1232.

Ehrlich, P.R., White, R.R. *et al.* (1975) Checkerspot butterflies: a historical perspective. *Science* 188, 221–228.

Ehrman, L. (1966) Mating success and genotype frequency in *Drosophila*. *Animal Behaviour* 14, 332–339.

Ehrman, L. (1970) Mating advantage of rare males in *Drosophila*. *Proceedings of the National Academy of Sciences USA* 65, 345–348.

Eibl-Eibesfeldt, I. (1970) *Ethology: the Biology of Behavior*. New York, New York, USA: Holt, Rinehart and Winston.

Eichhorn, O. (1969) Problems of the determination of morphs of the genus *Dreyfusia* CB (Homoptera, Adelgidae). *Zeitschrift für angewandte Entomologie* 64, 437–446.

Eickwort, K.R. (1977) Population dynamics of a relatively rare species of milkweed beetle (*Labidomera*). *Ecology* 58, 527–538.

Eidt, D.T. and Thurston, G.S. (1995) Physical deterrents to infection by entomopathogenic nematodes in wireworms (Coleoptera: Elateridae) and other soil insects. *The Canadian Entomologist* 127, 423–429.

Eiseley, L.C. (1961) *Darwin's Century*. New York, New York, USA: Doubleday.

Eisikowich, D. and Galil, J. (1971) Effect of wind on the pollination of *Pancratium maritimum* L. (Amaryllidaceae) by hawk moths (Lepidoptera: Sphingidae). *Journal of Animal Ecology* 40, 673–678.

Eldridge, B.F. and Edman, J.D. (2003) *Medical Entomology*. New York, New York, USA: Springer.

Eliopoulos, P.A. (2006) Life tables of *Venturia canescens* (Hymenoptera: Ichneumonidae) parasitising the Mediterranean flour moth (Lepidoptera: Pyralidae). *Journal of Economic Entomology* 99, 237–243.

Elkinton, J.S. and Liebhold, A.M. (1990) Population dynamics of gypsy moth in North America. *Annual Review of Entomology* 35, 571–596.

Elkinton, J.S., Healy, W.M. *et al.* (1996) Interactions among gypsy moths, white-footed mice, and acorns. *Ecology* 77, 2332–2342.

Ellington, C.P. (1991) Limitations on animal flight performance. *The Journal of Experimental Biology* 160, 71–91.

Ellington, C.P. (1995) Unsteady aerodynamics of insect flight. *Symposium of the Society for Experimental Biology* 49, 109–129.

Elliott, S.E. (2009) Surplus nectar available for subalpine bumble bee colony growth. *Environmental Entomology* 38, 1680–1689.

Ellis, P.E., Carlisle, D.B. *et al.* (1965) Desert locusts: sexual maturity delayed by feeding on senescent vegetation. *Science* 149, 546–547.

Ellis, S.A. and Scatcherd, J.E. (2007) Bean seed fly (*Delia platura*, *Delia florilega*) and onion fly (*Delia antiqua*) incidence in England and an evaluation of chemical and biological control options. *Annals of Applied Biology* 151, 259–267.

Ellner, S. and Turchin, P. (1995) Chaos in a noisy world: new methods and evidence from time-series analysis. *The American Naturalist* 145, 343–375.

Elton, C.S. (1927) *Animal Ecology*. London, UK: Sidgwick and Jackson.

Elton, C.S. (1949) Population interspersion: an essay on animal community patterns. *Journal of Ecology* 37, 1–23.

Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. London, UK: Methuen.

Elton, C.S. (1966) *The Pattern of Animal Communities*. London, UK: Methuen.

Elton, C.S. and Miller, R.S. (1954) The ecological survey of animal communities with a practical system of classifying habitats by structural characters. *Journal of Ecology* 42, 460–496.

Embree, D.G. (1991) The winter moth *Operophtera brumata* in eastern Canada, 1962–1988. *Forest Ecology and Management* 39, 47–54.

Emlen, D.J., Marangelo, J. *et al.* (2005) Diversity in the weapons of sexual selection: horn evolution in the beetle genus *Onthophagus* (Coleoptera: Scarabaeidae). *Evolution* 59, 1060–1084.

Emlen, J.M. (1968) Selection for the sex-ratio. *The American Naturalist* 102, 589–591.

Emmel, T.C. (1991) *Butterflie*s. New York, New York, USA: Friedman.

Endler, J.A. (1986) *Natural Selection in the Wild*. Princeton, New Jersey, USA: Princeton University Press.

Endler, J.A. (1992) Signals, signal conditions, and the direction of evolution. *The American Naturalist* 139, S125–S153.

Endler, J.A. and McLellan, T. (1988) The process of evolution: towards a newer synthesis. *Annual Review of Ecology and Systematics* 19, 395–421.

Enfjall, K. and Leimar, O. (2005) Density-dependent dispersal in the Glanville fritillary, *Melitaea cinxa*. *Oikos* 108, 465–472.

English-Loeb, G.M., Karban, R. *et al*. (1990) Arctiid larvae survive attack by a tachinid parasitoid and produce viable offspring. *Ecological Entomology* 15, 361–362.

Enright, J.T. (1976) Climate and population regulation, the biogeographer's dilemma. *Oecologia* 24, 295–310.

Erdmann, G.R. (1987) Antibacterial action of myiasis-causing flies. *Parasitology Today* 3, 214–216.

Escalante, A.A., Barrio, E. *et al*. (1995) Evolutionary origin of human and primate malarias: evidence from the circumsporozoite protein gene. *Molecular Biology and Evolution* 12, 616–626.

Esch, H.E., Zhang, S. *et al*. (2001) Honey bee dances communicate distances by measuring optic flow. *Nature* 411, 581–583.

Espino, L., Way, M.O. *et al*. (2007) Most susceptible stage of rice panicle development to *Oebalus pugnax* (Hemiptera: Pentatomidae). *Journal of Economic Entomology* 100, 1282–1290.

Estoup, A., Scholl, A. *et al*. (1995) Monandry and polyandry in bumble bees (Hymenoptera: Bombinae) as evidenced by highly variable microsatellites. *Molecular Ecology* 4, 89–93.

Evans, E.W. and England, S. (1996) Indirect interactions in biological control of insects: pests and natural enemies in alfalfa. *Ecological Applications* 6, 920–930.

Evans, H.E. (1970) *Life on a Little Known Planet*. London, UK: Deutsch.

Evans, W.G. and Kuster, J.E. (1980) The infrared receptive fields of *Melanophila acuminata* (Coleoptera: Buprestidae). *The Canadian Entomologist* 112, 211–216.

Ewald, P.W. (1983) Host-parasite relations, vectors, and the evolution of disease severity. *Annual Review of Ecology and Systematics* 14, 465–485.

Fabre, J.H. (1882) *Nouveaux Souvenirs Entomologiques: Études sur L'instincte et Les Moeurs des Insectes*. Paris, France: Delagrave.

Fabre, J.H. (1919) *The Mason Wasps*. London, UK: Hodder and Stoughton.

Faegri, K. and van der Pijl, L. (1978) *The Principles of Pollination Ecology*, 3rd edn. Oxford, UK: Pergamon.

Fagerstrom, T. and Wiklund, C. (1982) Why do males emerge before females? Protandry as a mating strategy in male and female butterflies. *Oecologia* 52, 164–166.

Fallis, S.P. and Snow, K.R. (1983) Distribution of the eggs of *Aedes punctor* (Diptera: Culicidae). *Ecological Entomology* 8, 139–144.

Fanello, C., Santolamazza, F. *et al*. (2002) Simultaneous identification of species and molecular forms of the *Anopheles gambiae* complex by PCR-RFLP. *Medical and Veterinary Entomology* 16, 461–464.

Fargo, W.S., Rensner, P.E. *et al*. (1988) Population dynamics in the squash bug (Heteroptera: Coreidae) – squash plant (Curcurbitales: Curcurbitaceae) system in Oklahoma. *Journal of Economic Entomology* 81, 1073–1079.

Farrell, B.D. (1998) "Inordinate fondness" explained: why are there so many beetles? *Science* 281, 555–559.

Farrow, R.A. (1981) Aerial dispersal of *Scelio fulgidus* (Hym.: Scelionidae), parasite of the eggs of grasshoppers and locusts (Orthoptera: Acrididae). *Entomophaga* 26, 349–355.

Fasolo, A.G. and Krebs, R.A. (2004) A comparison of behavioural change in *Drosophila* during exposure to thermal stress. *Biological Journal of the Linnean Society* 83, 197–205.

Fatouros, N.E., Huigens, M.E. *et al*. (2005) Butterfly's anti-aphrodisiac lures parasitic wasps. *Nature* 433, 704.

Favia, G., Lanfrancotti, A. *et al*. (2001) Molecular characterisation of ribosomal DNA (rDNA) polymorphisms discriminating among chromosomal forms of *Anopheles gambiae* s.s. *Insect Molecular Biology* 10, 19–23.

Federici, B.A. and Bigot, Y. (2003) Origin and evolution of polydnaviruses by symbiogenesis of insect DNA viruses in endoparasitic wasps. *Journal of Insect Physiology* 49, 419–432.

Fedorov, A.V. and Philander, S.G. (2000) Is El Niño changing? *Science* 288, 1997–2002.

Feener, D.H. (1981) Competition between ant species: outcome controlled by parasitic flies. *Science* 214, 815–817.

Feener, D.H. and Brown, B.V. (1997) Diptera as parasitoids. *Annual Review of Entomology* 42, 73–97.

Feeny, P.P. (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51, 565–581.

Feeny, P.P. (1976) Plant apparency and chemical defence. *Recent Advances in Phytochemistry* 10, 1–40.

Feldhaar, H. (2011) Bacterial symbionts as mediators of ecologically important traits of insect hosts. *Ecological Entomology* 36, 533–543.

Feliciangeli, M.D. (2004) Natural breeding places of phlebotomine sandflies. *Medical and Veterinary Entomology* 18, 71–80.

Felsenstein, J. (1981) Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* 35, 124–138.

Felt, E.P. (1937) Dissemination of insects by air currents. *Journal of Economic Entomology* 30, 458–461.

Feltwell, J. (1990) *The Silk Road: China to England*. Stroud, UK: Sutton Publishing.

Feng, H.-Q., Wu, K.-M. *et al.* (2005) Return migration of *Helicoverpa armigera* (Lepidoptera: Noctuidae) during autumn in northern China. *Bulletin of Entomological Research* 95, 361–370.

Fenster, C.B., Armbruster, W.S. *et al.* (2004) Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics* 35, 375–403.

Ferre, J. and van Rie, J. (2002) Biochemistry and genetics of insect resistance to *Bacillus thuringiensis*. *Annual Review of Entomology* 47, 501–533.

Ferro, D.N., Logan, J.A. *et al.* (1985) Colorado potato beetle temperature dependent growth and feeding rates. *Environmental Entomology* 14, 343–348.

Ferro, D.N., Tuttle, A.F. *et al.* (1991) Ovipositional and flight behavior of overwintered Colorado potato beetles. (Coleoptera: Chrysomelidae). *Environmental Entomology* 20, 1309–1314.

Fialho, R.F. and Schall, J.J. (1995) Thermal ecology of a malarial parasite and its insect vector: consequences for the parasite's success. *Journal of Animal Ecology* 64, 553–562.

Fields, P.G. and Korunic, Z. (2000) Diatomaceous earth to control *Cryptolestes ferrugineus* (Coleoptera: Cucujidae) in stored barley in farm granaries. *The Canadian Entomologist* 132, 247–258.

Filchak, K.E., Roethele, J.B. *et al.* (2000) Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. *Nature* 407, 739–742.

Finch, S. (1989) Ecological considerations in the management of *Delia* pest species in vegetable crops. *Annual Review of Entomology* 34, 117–137.

Finch, S. and Collier, R.H. (1983) Emergence of flies from overwintering populations of cabbage root fly pupae. *Ecological Entomology* 8, 29–36.

Finch, S. and Jones, T.H. (1989) An analysis of the deterrent effect of aphids on cabbage root flies (*Delia radicum*) egg-laying. *Ecological Entomology* 14, 387–391.

Finch, S. and Skinner, G. (1975) Dispersal of the cabbage root fly. *Annals of Applied Biology* 81, 1–19.

Fincke, O.M. (1992) Behavioural ecology of the giant damselflies of Barro Colorado Island, Panama (Odonata: Zygoptera: Pseudostigmatidae). In: Quintero Arias, D. and Aiello, A. (eds) *Insects of Panama and Mesoamerica: Selected Studies*. Oxford, UK: Oxford University Press, pp. 102–113.

Fineblum, W.L. and Rausher, M.D. (1997) Do floral pigmentation genes also influence resistance to enemies? The W locus in *Ipomoea purpurea*. *Ecology* 78, 1646–1654.

Finke, D.L. and Denno, R.F. (2003) Intra-guild predation relaxes enemy impacts on herbivore populations. *Ecological Entomology* 28, 67–73.

Finlay, C.J. (1886) Yellow fever, its transmission by the *Culex* mosquito. *The American Journal of Medical Science* 92, 395–409.

Finn, J.A. and Gittings, T. (2003) A review of competition in north temperate dung beetle communities. *Ecological Entomology* 28, 1–13.

Finney, D.J. (1947) *Probit analysis: A Statistical Treatment of the Sigmoid Response Curve*. Cambridge, UK: Cambridge University Press.

Firbank, L.G., Carter, N. *et al.* (eds) (1990) *The Ecology of Temperate Cereal Fields*. London, UK: Blackwell.

Fischer, A.G. (1960) Latitudinal variations in organic diversity. *Evolution* 14, 64–81.

Fisher, R.A. (1918) The correlation between relatives under the supposition of Mendelian inheritance. *Transactions of the Royal Society of Edinburgh* 52, 399–433.

Fisher, R.A. (1922) On the dominance ratio. *Proceedings of the Royal Society of Edinburgh* 42, 321–341.

Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*. Oxford, UK: Clarendon Press. Reprinted with additions by Dover Publications (1958).

Fisher, R.A. (1937) The wave of advance of advantageous genes. *Annals of Eugenics* 7, 355–369.

Fisher, R.A. (1941) Average excess and average effect of a gene substitution. *Annals of Eugenics* 11, 53–63.

Fisher, R.A. (1949) *The Theory of Inbreeding*. Edinburgh, UK: Oliver and Boyd.

Fisher, R.A., Corbet, A.S. *et al.* (1943) The relationship between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* 12, 42–58.

Fiske, W.F. (1910) Superparasitism: an important factor in the natural control of insects. *Journal of Economic Entomology* 3, 88–97.

Fitt, G.P. (1989) The ecology of *Heliothis* species in relation to agroecosystems. *Annual Review of Entomology* 34, 17–52.

Fitt, G.P. (1990) Variation in ovariole number and egg size of species of *Dacus* (Diptera: Tephritidae) and their relation to host specialisation. *Ecological Entomology* 15, 255–264.

Fitt, G.P. (1994) Cotton pest management: Part 3. An Australian perspective. *Annual Review of Entomology* 39, 543–562.

Fitzgerald, F.S. (1926) *The Great Gatsby*. London, UK: Penguin (1950 edn.).

Fitzgerald, T.D. (2008) Larvae of the fall webworm, *Hyphantria cunea*, inhibit cyanogenesis in *Prunus serotina*. *The Journal of Experimental Biology* 211, 671–677.

Fitzgerald, T.D. and Willer, D.E. (1983) Tent-building behavior of the eastern tent caterpillar *Malacosoma americanum* (Lepidoptera: Lasiocampidae). *Journal of the Kansas Entomological Society* 56, 20–31.

Fitzpatrick, M.J., Ben-Shahar, Y. *et al.* (2005) Candidate genes for behavioural ecology. *Trends in Ecology and Evolution* 20, 96–104.

Flanders, S.E. (1942) Abortive development in parasitic Hymenoptera induced by the food plant of the insect host. *Journal of Economic Entomology* 35, 834–835.

Flanders, S.E. (1945) The bisexuality of uniparental Hymenoptera, a function of the environment. *The American Naturalist* 79, 122–141.

Flanders, S.E. (1947) Elements of host discovery exemplified by the parasitic Hymenoptera. *Ecology* 28, 299–309.

Flanders, S.E. (1953) Predatism by the adult hymenopterous parasite and its role in biological control. *Journal of Economic Entomology* 46, 541–544.

Fleming, J.G.W. (1992) Polydnaviruses: mutualists and pathogens. *Annual Review of Entomology* 37, 401–425.

Fletcher, B.S. (1987) The biology of dacine fruit flies. *Annual Review of Entomology* 32, 115–144.

Flor, H.H. (1942) Inheritance of pathogenicity in *Melampsora lini*. *Phytopathology* 32, 653–669.

Foelker, C.J. (2016) Beneath the bark: associations among *Sirex noctilio* development, bluestain fungi, and pine host species in North America. *Ecological Entomology* 41, 676–684.

Foil, L.D. (1989) Tabanids as vectors of disease agents. *Parasitology Today* 5, 88–95.

Follett, P.A., Cantelo, W.W. *et al.* (1996) Local dispersal of overwintered Colorado potato beetles (Coleoptera: Chrysomelidae) determined by mark and recapture. *Environmental Entomology* 25, 1304–1311.

Foltz, J.L, Knight, F.B. *et al.* (1972) Numerical analysis of population fluctuations of the jack pine budworm. *Annals of the Entomological Society of America* 65, 82–89.

Fonseca, C.R. and Ganade, G. (1996) Asymmetries, compartments and null interactions in an Amazonian ant-plant community. *Journal of Animal Ecology* 65, 339–347.

Forbes, A.A., Hood, G.R. *et al.* (2010) Geographic and ecological overlap of parasitoid wasps associated with *Rhagoletis pomonella* (Diptera: Tephritidae) species complex. *Annals of the Entomological Society of America* 103, 908–915.

Force, D.C. (1974) Ecology of insect host–parasitoid communities. *Science* 184, 624–632.

Force, D.C. and Messenger, P.S. (1964) Developmental period, generation time, and longevity of three parasites of *Therioaphis maculata* (Buckton) reared at various constant temperatures. *Annals of the Entomological Society of America* 57, 405–413.

Ford, E.B. (1931) *Mendelism and Evolution*. London, UK: Methuen.

Ford, E.B. (1946) *Butterflies*. New Naturalist Series. London, UK: Collins.

Ford, E.B. (1955) *Moths*. New Naturalist Series. London, UK: Collins.

Ford, E.B. (1961) The theory of genetic polymorphism. *Symposia of the Royal Entomological Society of London* 1, 11–19.

Ford, E.B. (1975) *Ecological Genetics*, 4th edn. London, UK: Chapman and Hall.

Ford, H.D. and Ford, E.B. (1930) Fluctuation in numbers and its influence on variation, in *Melitaea aurinia*. *Transactions of the Entomological Society of London* 78, 345–351.

Forkner, R.E., Marquis, R.T. *et al*. (2004) Feeney revisited: condensed tannins as anti-herbivore defences in leaf-chewing herbivore communities of Quercus. *Ecological Entomology* 29, 174–187.

Forneck, A. and Huber, L. (2009) (A) sexual reproduction- a review of life cycles of grape phylloxera, *Daktulosphaira vitifoliae*. *Entomologia Experimentalis et Applicata* 131, 1–10.

Forrest, T.G. (1986) Oviposition and maternal investment in mole crickets (Orthoptera: Gryllotalpidae): effects of season, size, and senescence. *Annals of the Entomological Society of America* 79, 918–924.

Foster, J.E., Ohm, H.W. *et al*. (1991) Effectiveness of deploying single gene resistance in wheat for controlling damage by the Hessian fly (Diptera: Cecidomyiidae). *Environmental Entomology* 20, 964–969.

Fowler, S.V. and Lawton, J.H. (1985) Rapidly induced defences and talking trees: the Devil's advocate position. The American Naturalist 126, 181–195.

Fox, C.W. and Czesak, M.E. (2000) Evolutionary ecology of progeny size in arthropods. *Annual Review of Entomology* 45, 341–369.

Fox, L.R. (1975) Cannibalism in natural populations. *Annual Review of Ecology and Systematics* 6, 87–106.

Foyer, C.H., Noctor, G. *et al*. (2007) An evaluation of the costs of making specific secondary metabolites: does the yield penalty incurred by host plant resistance to insects result from competition for resources? *International Journal of Pest Management* 53, 175–182.

Fraenkel, G.S. (1959) The raison d'être of secondary plant substances. *Science* 129, 1466–1470.

Frank, J.H. (1967) The effect of pupal predators on a population of the winter moth, *Operophtera brumata* (L.) (Hydriomenidae). *Journal of Animal Ecology* 36, 611–621.

Frank, J.H., Walker, T.J. *et al*. (1996) The introduction, establishment, and spread of *Ormia depleta* in Florida. *Biological Control* 6, 368–377.

Frank, S.D., Shrewsbury, P.M. *et al*. (2010) Effects of alternative food on cannibalism and herbivore suppression by carabid larvae. *Ecological Entomology* 35, 61–68.

Frankham, R. (1995) Inbreeding and extinction: a threshold effect. *Conservation Biology* 9, 792–799.

Franzen, M. and Nilsson, S.G. (2007) What is the required minimum landscape size for dispersal studies? *Journal of Animal Ecology* 76, 1224–1230.

Freckleton, R.P., Watkinson, A.R. *et al*. (2006) Census error and the detection of density dependence. *Journal of Animal Ecology* 75, 837–851.

Free, J.B. (1970) The flower constancy of bumblebees. *Journal of Animal Ecology* 39, 395–402.

Free, J.B. (1993) *Insect Pollination of Crops*. London, UK: Academic Press.

Freeman, B.E. (1964) A population study of *Tipula* species (Diptera, Tipulidae). *Journal of Animal Ecology* 33, 129–140.

Freeman, B.E. (1965) An investigation during winter of the distribution of the white clover seed weevil, *Apion dichroum* Bedel (Col. Curculionidae). *Journal of Applied Ecology* 2, 105–113.

Freeman, B.E. (1967a) The biology of the white clover seed weevil *Apion dichroum* Bedel (Col. Curculionidae). *Journal of Applied Ecology* 4, 535–552.

Freeman, B.E. (1967b) Studies on the ecology of larval Tipulinae (Diptera, Tipulidae). *Journal of Animal Ecology* 36, 123–146.

Freeman, B.E. (1968) Studies on the ecology of adult Tipulidae (Diptera) in southern England. *Journal of Animal Ecology* 37, 339–362.

Freeman, B.E. (1973a) Preliminary studies on the population dynamics of *Sceliphron assimile* Dahlbom (Hymenoptera: Sphecidae) in Jamaica. *Journal of Animal Ecology* 42, 173–182.

Freeman, B.E. (1973b) A technique for collecting arboreal, social wasps nests. *Annals of the Entomological Society of America* 66, 916–917.

Freeman, B.E. (1974) The distribution in Jamaica of the mud wasp *Sceliphron assimile* Dahlbom (Sphecidae) and its associates. *Caribbean Journal of Science* 14, 115–124.

Freeman, B.E. (1976) A spatial approach to insect population dynamics. *Nature* 260, 240–241.

Freeman, B.E. (1977) Aspects of the regulation of size of the Jamaican population of *Sceliphron assimile* Dahlbom (Hymenoptera; Sphecidae). *Journal of Animal Ecology* 46, 231–247.

Freeman, B.E. (1980) A population study in Jamaica on adult *Sceliphron assimile* (Dahlbom) (Hymenoptera: Sphecidae). *Ecological Entomology* 5, 19–30.

Freeman, B.E. (1981a) The dynamics in Trinidad of *Trypoxylon palliditarse* Saussure: a Thompsonian population? *Journal of Animal Ecology* 50, 563–572.

Freeman, B.E. (1981b) Parental investment in a solitary wasp. *The American Naturalist* 117, 357–362.

Freeman, B.E. (1981c) Parental investment and its ecological consequences in the solitary wasp *Sceliphron assimile* (Dahlbom) (Sphecidae). *Behavioral Ecology and Sociobiology* 9, 261–268.

Freeman, B.E. (1982) The comparative distribution and population dynamics in Trinidad of two Sceliphron spp. (Hymenoptera: Sphecidae). *Biological Journal of the Linnean Society* 17, 343–360.

Freeman, B.E. and Adams, C.A. (1972) The spatial and temporal distribution of adult Tipulidae (Diptera) at Hothfield Heath, Kent. *Journal of Animal Ecology* 41, 537–551.

Freeman, B.E. and Geoghagen, A. (1987) Size and fecundity in the Jamaican gall-midge *Asphondylia boerhaaviae*. *Ecological Entomology* 12, 239–249.

Freeman, B.E. and Geoghagen, A. (1989) A population study in Jamaica on the gall midge *Asphondylia boerhaaviae*: a contribution to spatial dynamics. *Journal of Animal Ecology* 58, 367–382.

Freeman, B.E. and Ittyeipe, K. (1976) Field studies on the cumulative response of *Melittobia* sp. (*hawaiiensis* complex) (Eulophidae) to varying host densities. *Journal of Animal Ecology* 45, 415–423.

Freeman, B.E. and Ittyeipe, K. (1982) Morph determination in *Melittobia*, a eulophid wasp. *Ecological Entomology* 7, 355–363.

Freeman, B.E. and Ittyeipe, K. (1993) The natural dynamics of the eulophid parasitoid *Melittobia australica*. *Ecological Entomology* 18, 129–140.

Freeman, B.E. and Jayasingh, D.B. (1975a) Population dynamics in Jamaica of *Pachodynerus nasidens* (Hymenoptera: Eumenidae). *Oikos* 26, 86–91.

Freeman, B.E. and Jayasingh, D.B. (1975b) Factors controlling the distribution in Jamaica of *Pachodynerus nasidens* (Latr.) (Hymenoptera: Eumenidae). *Biological Journal of the Linnean Society* 7, 231–242.

Freeman, B.E. and Johnston, B.Y. (1978a) The biology in Jamaica of the adults of the sphecid wasp *Sceliphron assimile* Dahlbom. *Ecological Entomology* 3, 39–52.

Freeman, B.E. and Johnston, B.Y. (1978b) Gregarious roosting in the sphecid wasp *Sceliphron assimile* (Dahlbom). *Annals of the Entomological Society of America* 71, 435–441.

Freeman, B.E. and Mulder, W.H. (2019) Insect dynamics in heterogeneous environments and the relevance of retrospective life tables and cyclic budgets: an integrated approach. *Journal of Entomological Science* 54, 325.

Freeman, B.E. and Parnell, J.R. (1973) Mortality of *Sceliphron assimile* Dahlbom (Sphecidae) caused by the eulophid *Melittobia chalybii* Ashmead. *Journal of Animal Ecology* 42, 779–784.

Freeman, B.E. and Smith, D.C. (1990) Variation of density-dependence with spatial scale in the leaf-mining fly *Liriomyza commelinae* (Diptera, Agromyzidae). *Ecological Entomology* 15, 265–274.

Freeman, B.E. and Taffe, C.A. (1974) Population dynamics and nesting behaviour of *Eumenes colona* (Hymenoptera) in Jamaica. *Oikos* 25, 388–394.

Freeman, B.E. and Wimble, R.H. (1970) The use of Malathion to control the white clover seed weevil, *Apion dichroum* Bedel (Col., Curculionidae). *Plant Pathology* 19, 119–122.

Freeman, J.A. (1945) Studies on the distribution of insects by aerial currents. *Journal of Animal Ecology* 14, 128–154.

Frid, I. and Myers, G. (2002) Thermal ecology of western tent caterpillars *Malacosoma californicum pluviale* and infection by nucleopolyhedrovirus. *Ecological Entomology* 27, 665–673.

Frohlich, M.W. (1976) The appearance of vegetation in ultraviolet light; absorbing flowers, reflecting backgrounds. *Science* 194, 839–841.

Fulhorst, C.F., Hardy, J.L. *et al.* (1994) Natural vertical transmission of Western Equine Encephalomyelitis Virus in mosquitoes. *Science* 263, 676–678.

Fulton, J.P., Gergerich, R.C. *et al.* (1987) Beetle transmission of plant viruses. *Annual Review of Phytopathology* 25, 111–123.

Furuta, K. (1986) Host preference and population dynamics in an autumnal population of the maple aphid, *Periphyllus californiensis* Shinje (Homoptera: Aphididae). *Journal of Applied Entomology* 102, 93–100.

Fuxa, J.R. (1987) Ecological considerations for the use of entomopathogens in IPM. *Annual Review of Entomology* 32, 225–251.

Fye, R.E., Hopkins, A.R. *et al.* (1959) The distance into woods along a cotton field at which the boll weevil hibernates. *Journal of Economic Entomology* 52, 310–312.

Gage, K.L. and Kosoy, M.Y. (2005) Natural history of plague: perspectives from more than a century. *Annual Review of Entomology* 50, 505–528.

Gange, A.C. and Brown, V.K. (eds) (1997) *Multitrophic Interactions in Terrestrial Ecosystems*. London, UK: Blackwell Science.

Gardner, S.M. and Dixon, A.G.F. (1985) Plant structure and the foraging success of *Aphidius rhopalosiphi* (Hymenoptera: Aphidiidae). *Ecological Entomology* 10, 171–179.

Gargiullo, P.M. and Berisford, C.W. (1983) Life tables for the Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock) and the pitch pine tip moth, *Rhyacionia rigidana* (Fernald) (Lepidoptera: Tortricidae). *Environmental Entomology* 12, 1391–1402.

Garraway, E. (1983) The Population Dynamics of Bark Beetles in Jamaican Forest Plantations. Doctoral thesis, University of the West Indies.

Garraway, E. and Freeman, B.E. (1981) Studies on the population dynamics of the Juniper bark beetle (*Phloeosinus neotropicus*) in Jamaica. *Oikos* 36, 363–368.

Garraway, E. and Freeman, B.E. (1990) The population dynamics of *Ips grandicollis* (Eichhoff) (Coleoptera: Scolytidae) in Jamaica. *The Canadian Entomologist* 122, 217–227.

Garraway, E., Bailey, A.J.A. *et al.* (1993a) Contribution to the ecology and conservation biology of the endangered *Papilio homerus* (Lepidoptera: Papilionidae). *Tropical Lepidoptera* 4, 83–91.

Garraway, E., Bailey, A.J.A. *et al.* (1993b) Studies on the Jamaican kite swallowtail, *Eurytides (Protesilaus) marcellinus* (Lepidoptera: Papilionidae). *Tropical Lepidoptera* 4, 151–154.

Garraway, E., Bailey, A.J.A. *et al.* (2008) Population studies and conservation of Jamaica's endangered swallowtail butterfly Papilio (Pterourus) homerus. *Journal of Insect Conservation* 12, 383–397.

Garrett, L. (1994) *The Coming Plague: Newly Emerging Diseases in a World out of Balance*. New York, New York, USA: Penguin.

Garrett-Jones, C. (1964) Prognosis for interruption of malaria transmission through assessment of the mosquito's vectorial capacity. *Nature* 204, 1173–1175.

Garibaldi, L.A., Steffan-Dewenter, I. *et al.* (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339, 1608–1611.

Gary, R.E. and Foster, W.A. (2004) *Anopheles gambiae* feeding and survival on honeydew and extra-floral nectar of peridomestic plants. *Medical and Veterinary Entomology* 18, 102–107.

Gaston, K.J. (1988) Patterns of local and regional dynamics of moth populations. *Oikos* 53, 49–57.

Gaston, K.J. (1994) *Rarity*. London, UK: Chapman and Hall.

Gaston, K.J. (1998) Species-range size distributions: products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society B* 353, 219–230.

Gaston, K.J. (2009a) Geographic range limits of species. *Proceedings of the Royal Society B* 276, 1391–1393.

Gaston, K.J. (2009b) Geographic range limits: achieving synthesis. *Proceedings of the Royal Society B* 276, 1395–1406.

Gaston, K.J. and Blackburn, T.M. (2000) *Pattern and Process in Macroecology*. Oxford, UK: Blackwell Science.

Gaston, K.J. and Lawton, J.H. (1988) Patterns in the distribution and abundance of insect populations. *Nature* 331, 709–712.

Gaston, K.J. and Lawton, J.H. (1991) Insect herbivores on bracken do not support the core-satellite hypothesis. *The American Naturalist* 134, 761–777.

Gatehouse, A.G. (1987) Migration: a behavioural process with ecological consequences. *Antenna* 11, 10–12.

Gatehouse, A.G. (1997) Behavior and ecological genetics of wind-borne migration by insects. *Annual Review of Entomology* 42, 475–502.

Gauld, I.D. and Bolton, B. (1991) *The Hymenoptera*. Oxford, UK: Oxford University Press.

Gauld, I.D. Gaston, K.J. *et al.* (1992) Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the "nasty" host hypothesis. *Oikos* 65, 353–357.

Gaum, W.G., Giliomee, J.H. *et al.* (1994) Life history and life tables of western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), on English cucumbers. *Bulletin of Entomological Research* 84, 219–224.

Gause, G.F. (1934) *The Struggle for Existence*. Baltimore, Maryland, USA: Williams and Wilkins.

Gavrilets, S. (1997) Hybrid zones with Dobzhansky-type epistatic selection. *Evolution* 51, 1027–1035.

Gavrilets, S. (1999) The dynamical theory of speciation in holey adaptive landscapes. *The American Naturalist* 154, 1–22.

Gavrilets, S., Li, H. *et al*. (2000) Patterns of parapatric speciation. *Evolution* 54, 1126–1134.

Gennard, D. (2007) *Forensic Entomology: An Introduction*. New York, New York, USA: Wiley.

Gentry, G.L. and Dyer, L.A. (2002) On the conditional nature of Neotropical caterpillar defences against their natural enemies. *Ecology* 83, 3108–3119.

Georghiou, G.P. (1986) The magnitude of the resistance problem. In: *Pesticide Resistance: Strategies and Tactics for Management*. Washington, DC, USA: National Academic Press.

Georgis, R.A., Koppenhofer, M. *et al.* (2006) Successes and failures in the use of parasitic nematodes for pest control. *Biological Control* 38, 103–123.

Gergerich, R.C., Scott, H.A. *et al.* (1986) Evidence that ribonuclease in beetle regurgitant determines the transmission of plant viruses. *Journal of General Virology* 67, 367–370.

Gerling, D. (ed.) (1999) *Whiteflies: Their Bionomics, Pest Status and Management*. Andover, UK: Intercept Ltd.

Gevrey, M. and Worner, S.P. (2006) Prediction of global distribution of insect pest species in relation to climate by using an ecological informatics method. *Journal of Economic Entomology* 99, 979–986.

Ghiselin, M.T. (1974) *The Economy of Nature and the Evolution of Sex*. Berkeley, California, USA: University of California Press.

Giannini, A., Saravanan, R. *et al.* (2003) Oceanic forcing of Sahel rainfall on interannual to interdecadal timescales. *Science* 302, 1027–1030.

Gibson, R.W. and Pickett, J.A. (1983) Wild potato repels aphids by release of aphid alarm pheromone. *Nature* 302, 608–609.

Gilbert, F. and Owen, J. (1990) Size, shape, competition, and community structure in hover flies (Diptera: Syrphidae). *Journal of Animal Ecology* 59, 21–39.

Gilbert, L.E. (1984) The biology of butterfly communities. In: Vane-Wright, R.I. and Ackery, P.R. (eds) *The Biology of Butterflies*. Symposium of the Royal Entomological Society of London, No. 11. London, UK: Academic Press, pp. 41–54.

Gilbert, L.E. and Singer, M.C. (1975) Butterfly ecology. *Annual Review of Ecology and Systematics* 6, 365–397.

Gilbert, N. (1980) Comparative dynamics of a single-host aphid. 1. The evidence. *Journal of Animal Ecology* 49, 351–369.

Gilbert, N. (1984) Control of fecundity in *Pieris rapae*. (In three parts). *Journal of Animal Ecology* 53, 581–609.

Gilbert, N., Raworth, D.A. *et al.* (2010) One function of sex – an empirical study of genetic and ecological variation. *The Canadian Entomologist* 142, 601–628.

Giller, P.S. and Doube, B.M. (1989) Experimental analysis of inter- and intra-specific competition in dung beetle communities. *Journal of Animal Ecology* 58, 129–142.

Gillespie, J.H. (1984) Pleiotropic overdominance and the maintenance of genetic variation in polygenic characters. *Genetics* 107, 321–330.

Gillespie, S.D., Carrero, K. *et al.* (2015) Relationship between parasitism, bumble bee foraging behaviour and pollination service to *Trifolium pratense* flowers. *Ecological Entomology* 40, 650–653.

Gillies, M.T. (1980) The role of carbon dioxide in host-finding by mosquitoes (Diptera: Culicidae): a review. *Bulletin of Entomological Research* 70, 525–532.

Gillman, M. and Hails, R. (1997) *An Introduction to Ecological Modelling*: *Putting Practice into Theory*. Oxford, UK: Blackwell.

Gillooly, J.F., Brown, J.H. *et al.* (2001) Effects of size and temperature on metabolic rate. *Science* 293, 2248–2251.

Gillott, C. (2003) Male accessory gland secretions: modulators of female reproductive physiology and behavior. *Annual Review of Entomology* 48, 185–200.

Gillott, C. (2005) *Entomology*, 3rd edn. Dordrecht, Germany: Springer.

Gilpin, M.E. (1973) Do hares eat lynx? *The American Naturalist* 107, 727–730.

Gimelfarb, A. (1992) Pleiotropy and multilocus polymorphisms. *Genetics* 130, 223–227.

Ginzburg, L.R. and Taneyhill, D.E. (1994) Population cycles of forest Lepidoptera: a maternal effect hypothesis. *Journal of Animal Ecology* 63, 79–92.

Gittleman, J.L. and Luh, H-K. (1992) On comparing comparative methods. *Annual Review of Ecology and Systematics* 23, 383–404.

Gleason, H.A. (1926) The individualistic concept of the plant associations. *American Midland Naturalist* 21, 92–110.

Glen, D.M. (1975) The effects of predators on the eggs of codling moth *Cydia pomonella*, in a cider-apple orchard in south-west England. *Annals of Applied Biology* 80, 115–119.

Glick, P.A. (1939) The distribution of insects, spiders and mites in the air. *Technical Bulletin of the United States Department of Agriculture* No. 673. Washington, DC, USA: US Department of Agriculture.

Godfray, H.C.J. (1994) *Parasitoids: Behavioural and Evolutionary Ecology*. Princeton, New Jersey, USA: Princeton University Press.

Godfray, H.C.J. and Hassell, M.P. (1989) Discrete and continuous insect populations in tropical environments. *Journal of Animal Ecology* 58, 153–174.

Godfray, H.C.J. and Muller, C.B. (1998) Host-parasitoid dynamics. In: Dempster, J.P. and McLean, I.F.G. (eds) *Insect Populations in Theory and Practice*. Dordrecht, Germany: Kluwer Academic Publishers, pp.135–165.

Godfray, H.C.J., Hassell, M.P. *et al*. (1994) The population dynamic consequences of phenological asynchrony between parasitoids and their hosts. *Journal of Animal Ecology* 63, 1–10.

Goldsworthy, G. and Joyce, M. (2001) Physiology and endocrinology of flight. In: Woiwod, I.P., Reynolds, D. R. *et al*. (eds) *Insect Movement: Mechanisms and Consequences*. Wallingford, UK: CAB International, pp. 159–181.

Gols, R., Bukovinszky, T. *et al*. (2005) Reduced foraging efficiency of a parasitoid under habitat complexity: implications for population stability and species coexistence. *Journal of Animal Ecology* 74, 1059–1068.

Gonzalez-Santoyo, I. and Cordoba-Aguilar, A. (2012) Phenoloxidase: a key component of the insect immune system. *Entomologia Experimentalis et Applicata* 142, 1–16.

Goodwin, B.J. and Fahrig, L. (2002) How does landscape structure influence landscape connectivity? *Oikos* 99, 552–570.

Gorb, E. and Gorb, S. (2003) *Seed Dispersal by Ants in Deciduous Forest Ecosystems*. Berlin, Germany: Springer.

Gordon, S.P., Kokko, H. *et al*. (2015) Colour polymorphism torn apart by opposing positive frequency-dependent selection, yet maintained in space. *Journal of Animal Ecology* 84, 1555–1564.

Gotelli, N.J. (1991) Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis. *The American Naturalist* 138, 768–776.

Gotwald, W.H. (1995) *The Biology of Social Predation*. Ithaca, New York, New York, USA: Cornell University Press.

Goudge, T.A. (1961) *The Ascent of Life*. London, UK: Allen and Unwin.

Gould, F. (1991) The evolutionary potential of crop pests. *American Scientist* 79, 496–507.

Gould F. (1998) Sustainability of transgenic insecticidal cultivars: integrating pest genetics and ecology. *Annual Review of Entomology* 43, 701–726.

Gould, F., Holtzman, G. *et al*. (1980) Genetic variation in predatory and cannibalistic tendencies of *Heliothis virescens* strains. *Annals of the Entomological Society of America* 73, 243–250.

Gould, S.J. and Lewontin, R.C. (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society B* 205, 581–598.

Goulson, D. (2003) *Bumble Bees: their Behaviour and Ecology*. Oxford, UK: Oxford University Press.

Goulson, D. and Owen, D.F. (1997) Long-term studies of the *medionigra* polymorphism in the moth *Panaxia dominula*: a critique. *Oikos* 80, 613–617.

Grabenweger, G. and Lethmeyer, C. (1999) Occurrence and phenology of parasitic Chalcidoidea on the horse chestnut leafminer, *Cameraria ohridella* Deschka and Dimic (Lep., Gracillariidae). *Journal of Applied Entomology* 123, 257–260.

Graf, B., Hopli, H.U. *et al*. (2002) The apple sawfly, *Hoplocampa testudinea*: egg development and forecasting of egg hatch. *Entomologia Experimentalis et Applicata* 105, 55–60.

Grafton-Cardwell, E.E., Lee, J.E. *et al*. (2006) Role of two insect growth regulators in integrated pest management of citrus scales. *Journal of Economic Entomology* 99, 733–744.

Granett, J. and Timper, P. (1987) Demography of grape phylloxera, *Daktulosphaira vitifoliae* (Homoptera: Phylloxeridae), at different temperatures. *Journal of Economic Entomology* 80, 327–329.

Granett, J., Walker, M.A. *et al.* (2001) Biology and management of grape phylloxera. *Annual Review of Entomology* 46, 387–412.

Grass, G. (1978) *The Flounder*. Translated by Manheim, R. London, UK: Secker and Warburg.

Grassly, N.C. and Fraser, C. (2008) Mathematical models of infectious disease transmission. *Nature Reviews Microbiology* 6, 477–487.

Graunt, J. (1662) *Natural and Political Observations Mentioned in a Following Index, and Made upon the Bills of Mortality*. London, UK: Roycroft.

Graur, D. (1985) Gene diversity in Hymenoptera. *Evolution* 39, 190–199.

Gray, B. (1972) Economic tropical forest entomology. *Annual Review of Entomology* 17, 313–354.

Gray, M.E. and Tollefson, J.J. (1987) Influence of tillage on western and northern corn rootworm (Coleoptera: Chrysomelidae) egg populations, larval populations and root damage. *Journal of Economic Entomology* 80, 911–915.

Grayson, J., Edmunds, M. *et al.* (1991) Carotenoids and coloration of poplar hawk moth caterpillars, *Laothoe populi*. *Biological Journal of the Linnean Society* 42, 457–466.

Greathead, D.J. (1986) Parasitoids in classical biological control. In: Waage, J.K. and Greathead, D.J. (eds) *Insect Parasitoids*. London, UK: Academic Press, pp. 289–318.

Green, A.A. and Kane, J. (1954) The control of blowflies infesting slaughter houses. 3. Large scale experiments at a domestic refuse depot. *Annals of Applied Biology* 41, 165–173.

Green, J.H.S. (1957) William Charles Wells FRS (1757–1817). *Nature* 179, 997–999.

Greenleaf, S.S., Williams, N.M. *et al.* (2007) Bee foraging ranges and their relationship to body size. *Oecologia* 153, 589–596.

Greenslade, P.J.M. (1983) Adversity selection and the habitat templet. *The American Naturalist* 122, 252–365.

Griffiths, D. (1992) Size, abundance, and energy use in communities. *Journal of Animal Ecology* 61, 307–315.

Griffitts, J.S., Whitacre, J.L. *et al.* (2001) Bt toxin resistance from loss of a putative carbohydrate-modifying enzyme. *Science* 293, 860–864.

Grilli, M.P. and Bruno, M. (2007) Regional abundance of a planthopper pest: the effect of host patch area and configuration. *Entomologia Experimentalis et Applicata* 122, 133–143.

Grimaldi, D. and Engel, M.S. (2005) Evolution of Insects. Cambridge, UK: Cambridge University Press.

Grimble, D.G. and Knight, F.B. (1970) Life tables and mortality factors for *Saperda inornata* (Coleoptera: Cerambycidae). *Annals of the Entomological Society of America* 63, 1309–1319.

Grimble, D.G. and Knight, F.B. (1971) Mortality factors for *Oberea schaumii* (Coleoptera: Cerambycidae). *Annals of the Entomological Society of America* 64, 1417–1420.

Grime, J.P. (1974) Vegetational classification by means of strategies. *Nature* 250, 26–31.

Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111, 1169–1194.

Grimm, E.C., Jacobson, G.L. *et al.*(1993) A 50,000-year record of climate oscillations from Florida and its temporal correlation with the Heinrich Events. Science 261, 198–200.

Grimm, V. and Wissel, C. (1997) Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109, 323–334.

Grinnell, J. (1922) The role of the "accidental". *Auk* 39, 373–380.

Gripenberg, S. and Roslin, T. (2007) Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. *Oikos* 116, 181–188.

Gripenberg, S. and Roslin, T. (2008) Neither the devil nor the deep blue sea: larval mortality factors fail to explain the abundance and distribution of *Tischeria ekebladella*. *Ecological Entomology* 33, 346–356.

Gripenberg, S., Morrien, E. *et al.* (2007) Resource selection by female moths in a heterogeneous environment: what is a poor girl to do? *Journal of Animal Ecology* 76, 854–865.

Gröbler, B.C. and Lewis, O.T. (2008) Response of native parasitoids to a range-expanding host. *Ecological Entomology* 33, 453–463.

Groden, E. and Casagrande, R.A. (1986) Population dynamics of the Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) on *Solanum berthaultii*. *Journal of Economic Entomology* 79, 91–97.

Gross, L. (1996) How Charles Nicolle of the Pasteur Institute discovered that epidemic typhus is transmitted by lice: reminiscences from my years at the Pasteur Institute in Paris. *Proceedings of the National Academy of Sciences USA* 93, 10539–10540.

Gross, P. (1991) Influence of target pest feeding niche on success rates in classical biological control. Environmental Entomology 20, 1217–1227.

Gross, P. (1993) Insect behavioral and morphological defenses against parasitoids. *Annual Review of Entomology* 38, 251–273.

Grossmueller, D.W. and Lederhouse, R.C. (1985) Oviposition site selection: an aid to rapid growth and development in the tiger swallowtail butterfly, *Papilio glaucus*. *Oecologia* 66, 68–73.

Grove, S.J. (2002) Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics* 33, 1–23.

Grundy, P.R. (2007) Utilising the assassin bug, *Pristhesancus plagipennis* (Hemiptera: Reduviidae), as a biological control agent within an integrated pest management programme for *Helicoverpa* spp. (Lepidoptera: Noctuidae) and *Creontiades* spp. (Hemiptera: Miridae) in cotton. *Bulletin of Entomological Research* 97, 281–290.

Grüter, C. and Farina, W.M. (2008) The honey bee waggle dance: can we follow the steps? *Trends in Ecology and Evolution* 24, 242–247.

Grüter, C., Balbuena, M.S. *et al.* (2008) Informational conflicts created by the waggle dance. *Proceedings of the Royal Society B* 275, 1321–1327.

Guédot, C., Bosch, J. *et al.* (2009) Relationship between body size and homing ability in the genus *Osmia* (Hymenoptera: Megachilidae). *Ecological Entomology* 34, 158–161.

Guerenstein, P.G. and Hildebrand, J.G. (2008) Roles and effects of environmental carbon dioxide in insect life. *Annual Review of Entomology* 53, 161–178.

Guerin, P.M. and Stadler, E. (1984) Carrot fly cultivar preferences: some influencing factors. *Ecological Entomology* 9, 413–420.

Gui, L-Y., Xiu-Qin, H. *et al.* (2011) Validation of harmonic radar tags to study movement of Chinese citrus fly. *The Canadian Entomologist* 143, 415–422.

Guichard, S., Kriticos, D.J. *et al.* (2010) Evidence of active or passive downwind dispersal in mark-release-recapture of moths. *Entomologia Experimentalis et Applicata* 134, 160–169.

Gumbert, A. (2000) Color choices by bumble bees (*Bombus terrestris*): innate preferences and generalisation after learning. *Behavioral Ecology and Sociobiology* 48, 36–43.

Gündüz, E.A. and Douglas, A.E. (2009) Symbiotic bacteria enable an insect to use a nutritionally inadequate diet. *Proceedings of the Royal Society B* 276, 987–991.

Gunn, D.L. (1960) The biological background of locust control. *Annual Review of Entomology* 5, 279–300.

Gurevitch, J., Curtis, P.S. *et al.* (2001) Meta-analysis in ecology. *Recent Advances in Ecological Research* 32, 199–253.

Gurr, G.M. and Wratten, S.D. (1999) “Integrated biological control”: a proposal for enhancing success in biological control. *International Journal of Pest Management* 45, 81–84.

Gurtler, R.E., Segura, E.L. *et al.* (2003) Congenital transmission of *Trypanosoma cruzi* infection in Argentina. *Emerging Infectious Diseases* 9, 29–32.

Gutierrez, A.P., Pizzamiglio, M.A. *et al.* (1986) Analysis of diapause induction and termination in *Pectinophora gossypiella* in Brazil. *Environmental Entomology* 15, 495–500.

Guy, J. (1988) *Tudor England*. Oxford, UK: Oxford University Press.

Gwynne, D.T. (1984) Courtship feeding increases female reproductive success in bushcrickets. *Nature* 307, 361–363.

Gwynne, D.T. (2008) Sexual conflict over nuptial gifts in insects. *Annual Review of Entomology* 53, 83–101.

Haag, C.R., Saastamoinen, M. *et al.* (2005) A candidate locus for variation in dispersal rate in a butterfly metapopulation. *Proceedings of the Royal Society B* 272, 2449–2456.

Habel, J.C. and Schmitt, T. (2009) The genetic consequences of different dispersal behaviours in lycaenid butterfly species. *Bulletin of Entomological Research* 99, 513–523.

Hacker, S.D. and Bertness, M.D. (1996) Trophic consequences of a positive plant interaction. *The American Naturalist* 148, 559–575.

Haeckel, E.H.P.A. (1866) *Generelle Morphologie der Organismen*. Berlin, Germany: Georg Reimer.

Haeckel, E.H.P.A. (1870) Ueber Entwicklungsgang und Aufgabe der Zoologie. *Jenaische Zeitschrift* 5, 353–370.

Hagen, K.S. (1966) Dependence of the olive fly, *Dacus oleae*, larvae on symbiosis with *Pseudomonas savastanoi* for the utilization of olive. *Nature* 209, 423–424.

Hagen, S.B., Ims, R.A. *et al.* (2003) Density-dependent melanism in sub-arctic populations of winter moth larvae. *Ecological Entomology* 28, 659–665.

Haggstrom, H. and Larsson, S. (1995) Slow larval growth on a suboptimal willow results in high predation mortality in the leaf beetle *Galerucella lineola*. *Oecologia* 104 308–315.

Haigh, J.D. (2001) Climate variability and the influence of the Sun. *Science* 294, 2109–2111.

Hails, R.S. and Crawley, M.J (1992) Spatial density-dependence in a population of a cynipid gall-former *Andricus quercuscalicis*. *Journal of Animal Ecology* 61, 567–583.

Hairston, N.G. Jr and Hairston, N.G. Sr (1997) Does food web complexity eliminate trophic-level dynamics? *The American Naturalist* 149, 1001–1007.

Hairston, N.G., Smith, F.E. *et al.* (1960) Community structure, population control, and competition. *The American Naturalist* 94, 421–425.

Halbert, S.E. and Manjunath, K.L. (2004) Asian citrus psyllids (Sternorrhyncha: Psyllidae) and greening disease of citrus: a literature review and assessment of risk in Florida. *Florida Entomologist* 87, 330–353.

Haldane, J.B.S. (1922) Sex-ratio and unidirectional sterility in hybrid animals. *Journal of Genetics* 12, 101–109.

Haldane, J.B.S. (1932) *The Causes of Evolution*. London, UK: Longmans.

Haldane, J.B.S. (1948) The theory of a cline. *Journal of Genetics* 48, 277–284.

Haldane, J.B.S. (1949) Disease and evolution. Symposium sui fattori ecologici e genetici della speciazone negli animali. *Ricerca Scientifica* 19 (suppl.), 3–11.

Haldane, J.B.S. (1954) The statics of evolution. In: Huxley, J. *et al.* (eds) *Evolution as a Process*. London, UK: Allen and Unwin, pp. 109–121.

Haldane, J.B.S. (1956) The relation between density regulation and natural selection. *Proceedings of the Royal Society B* 145, 306–308.

Hall, R.W. and Ehler, L.E. (1979) Rate of establishment of natural enemies in classical biological control. *Entomological Society of America Bulletin* 25, 280–282.

Hallett, R.H. (2007) Host plant susceptibility to the swede midge (Diptera: Cecidomyiidae*)*. *Journal of Economic Entomology* 100, 1335–1343.

Halley, J.M. (1996) Ecology, evolution and 1/*f*-noise. *Trends in Ecology and Evolution* 11, 33–37.

Halley, J.M. and Inchausti, P. (2002) Lognormality in ecological time series. *Oikos* 99, 518–530.

Halstead, S.B. (2008) Dengue virus-mosquito interactions. *Annual Review of Entomology* 53, 273–291.

Hambäck, P.A. (2015) Getting the smell of it – odour cues structure pollinator networks. *Journal of Animal Ecology* 85, 315–317.

Hambäck, P.A., Vogt, M. *et al.* (2007) Top-down and bottom-up effects on the spatio-temporal dynamics of cereal aphids: testing scaling theory for local density. *Oikos* 116, 1995–2006.

Hamilton, W.D. (1964) The genetical evolution of social behaviour, 1. *Journal of Theoretical Biology* 7, 1–16.

Hamilton, W.D. (1967) Extraordinary sex ratios. *Science* 156, 477–488.

Hamilton, W.D. (1971) Geometry for the selfish herd. *Journal of Theoretical Biology* 31, 295–311.

Hamilton, W.D. (1972) Altruism and related phenomena, mainly in social insects. *Annual Review of Ecology and Systematics* 3, 193–232.

Hamilton, W.D. (1978) Evolution and diversity under bark. *Symposia of the Royal Entomological Society of London* 9, 154–175.

Hamilton, W.D. (1980) Sex versus non-sex versus parasite. *Oikos* 35, 282–290.

Hamilton, W.D. (1996) Narrow Roads of Gene Land, vol. 1. Oxford, UK: Freeman.

Hamilton, W.D. and May, R.M. (1977) Dispersal in stable habitats. *Nature* 269, 578–581.

Hamilton, W.D. and Zuk, M. (1982) Heritable true fitness and bright birds: a role for parasites. *Science* 218, 384–387.

Hammond, P.M. (1992) Species inventory. In: Groombridge, B. *Global Biodiversity: Status of the Earth's Living Resources*. London, UK: Chapman and Hall.

Hampson, N. (1990) *The Enlightenment*. London, UK: Penguin History.

Hanley, F. (1984) Time-budgeting and foraging strategy of the stoplight parrotfish *Sparisoma viride* Bonnaterre, in Jamaica. *Journal of Experimental Marine Biology and Ecology* 83, 159–177.

Hanski, I. (1982) Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38, 210–221.

Hanski, I. (1983) Coexistence of competitors in patchy environments. *Ecology* 64, 493–500.

Hanski, I (1985) Single-species population dynamics may contribute to long-term rarity and commonness. *Ecology* 66, 335–343.

Hanski, I. (1987) Carrion fly community dynamics: patchiness, seasonality and coexistence. *Ecological Entomology* 12, 257–266.

Hanski, I. (1990) Density dependence, regulation and variability in animal populations. *Philosophical Transactions of the Royal Society B* 330, 141–150.

Hanski, I. (1991) Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society* 42, 17–38.

Hanski, I. (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63, 151–162.

Hanski, I. (1998a) Spatial structure and dynamics of insect populations. In: Dempster, J.P. and McLean, I.F.G. (eds) (1998) *Insect Populations in Theory and Practice*. Dordrecht, Germany: Kluwer Academic Publishers, pp. 3–27.

Hanski, I. (1998b) Metapopulation dynamics. *Nature* 396, 41–49.

Hanski, I. and Gilpin, M.E. (1991) Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42, 3–16.

Hanski, I. and Gyllenberg, M. (1993) Two general metapopulation models and the core-satellite hypothesis. *The American Naturalist* 142, 17–41.

Hanski, I. and Woiwod, I.P. (1993) Spatial synchrony in the dynamics of moth and aphid populations. *Journal of Animal Ecology* 62, 656–668.

Hanski, I., Hansson, L. *et al.* (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology* 60, 353–367.

Hanski, I., Kuussaari, M. *et al.* (1994) Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology* 75, 747–762.

Hanski, I., Foley, P. *et al.* (1996) Random walks in a metapopulation: how much density dependence is necessary for long-term persistence? *Journal of Animal Ecology* 65, 274–282.

Hansson, L. (2003) Why ecology fails at application: should we consider variability more than regularity? *Oikos* 100, 624–627.

Harari, A.R., Ben-Yakir, D. *et al.* (1994) Mechanism of aggregation behavior in *Maladera matrida* Argaman (Coleoptera: Scarabaeidae). *Journal of Chemical Ecology* 20, 361–371.

Harbach, R.E. (2004) The classification of the genus *Anopheles* (Diptera: Culicidae): a working hypothesis of phylogenetic relationships. *Bulletin of Entomological Research* 94, 537–553.

Harcourt, D.G. (1957) Biology of the Diamondback Moth, *Plutella maculipennis* (Curt.) (Lepidoptera; Plutellidae), in Eastern Ontario. 2. *The Canadian Entomologist* 89, 554–564.

Harcourt, D.G. (1963) Population dynamics of *Leptinotarsa decemlineata* (Say) in Eastern Ontario 1. Spatial pattern and transformation of field counts. *The Canadian Entomologist* 95, 813–820.

Harcourt, D.G. (1964) Population dynamics of *Leptinotarsa decemlineata* (Say) in Eastern Ontario 2. Population and mortality estimation during six age intervals. *The Canadian Entomologist* 96, 1190–1198.

Harcourt, D.G. (1969) The development and use of life tables in the study of natural insect populations. *Annual Review of Entomology* 14, 175–196.

Harcourt, D.G. (1971) Population dynamics of *Leptinotarsa decemlineata* (Say) in eastern Ontario. 3. Major population processes. *The Canadian Entomologist* 103, 1049–1061.

Harcourt, D.G. (1990) Displacement of *Bathyplectes curculionis* (Thoms.) (Hymenoptera: Ichneumonidae) by *B. anurus* (Thoms.) in eastern Ontario populations of the alfalfa weevil, *Hypera postica* (Gryll.) (Coleoptera: Curculionidae). *The Canadian Entomologist* 122, 641–645.

Hardie, J., Gibson, G. *et al.* (2001) Insect behaviours associated with resource finding. In: Woiwod, I.P., Reynolds, D.R. *et al.* (eds), *Insect Movement: Mechanisms and Consequences*. Wallingford, UK: CAB International, pp. 87–109.

Hardin, G. (1960) The competitive exclusion principle. *Science* 131, 1292–1297.

Hardy, A.C. and Cheng, L. (1986) Studies in the distribution of insects by aerial currents. 3. Insect drift over the sea. *Ecological Entomology* 11, 283–290.

Hardy, G.H. (1908) Mendelian proportions in a mixed population. *Science* 28, 49–50.

Hardy, I.C.W. (1992) Non-binomial sex allocation and brood sex ratio variances in the parasitoid Hymenoptera. *Oikos* 65, 143–158.

Hardy, I.C.W. (1994) Polyandrous parasitoids: variety for variety's sake? *Trends in Ecology and Evolution* 9, 202–203.

Hardy, I.C.W., Dijkstra, L.J. *et al.* (1998) Patterns of sex ratio, virginity and developmental mortality in gregarious parasitoids. *Biological Journal of the Linnean Society* 64, 239–270.

Hare, J.D. (1990) Ecology and management of the Colorado potato beetle. *Annual Review of Entomology* 35, 81–100.

Hargrove, J.W. (2005) Extinction probabilities and times to extinction for populations of tsetse flies *Glossina* spp. (Diptera: Glossinidae) subjected to various control measures. *Bulletin of Entomological Research* 95, 13–21.

Hargrove, J.W., Torr, S.J. *et al.* (2003) Insecticide-treated cattle against tsetse (Diptera: Glossinidae): what governs success? *Bulletin of Entomological Research* 93, 203–217.

Harper, A.M. (1963) Sugar beet root aphid, *Pemphigus betae* Doane (Homoptera: Aphididae), in southern Alberta. *The Canadian Entomologist* 95, 863–873.

Harper, J.L. (1977) *The Population Biology of Plants*. London, UK: Academic Press.

Harrington, R. and Taylor, L.R. (1990) Migration for survival: fine scale population redistribution in an aphid, *Myzus persicae*. *Journal of Animal Ecology* 59, 1177–1193.

Harris, M.O., Sandanayaka, M. *et al.* (2001) Oviposition preferences of the Hessian fly and their consequences for survival and the reproductive potential of offspring. *Ecological Entomology* 26, 473–486.

Harris, M.O., Anderson, K.G. *et al.* (2006) Proximate cues for reduced oviposition by Hessian flies on wheat plants attacked by conspecific larvae. *Environmental Entomology* 35, 83–93.

Harrison, J.F. and Roberts, S.P. (2000) Flight, respiration and energetics. *Annual Review of Physiology* 62, 179–205.

Harrison, R.G. (1980) Dispersal polymorphism in insects. *Annual Review of Ecology and Systematics* 11, 95–118.

Harrison, S. (1989) Long-distance dispersal and colonization in the bay checkerspot butterfly, *Euphydryas editha bayensis*. *Ecology* 70, 1236–1243.

Harrison, S. (1991) Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society* 42, 73–88.

Harrison, S. (1994) Resources and dispersal as factors limiting a population of the tussock (*Orgyia vetusta*), a flightless defoliator. *Oecologia* 99, 27–34.

Harrison, S. and Hastings, A. (1996) Genetic and evolutionary consequences of metapopulation structure. *Trends in Ecology and Evolution* 11, 180–183.

Hart, A.J. and Bale, J.S. (1997) Evidence for the first strongly freeze tolerant insect found in the UK. *Ecological Entomology* 22, 242–245.

Hartman, M.J. and Hynes, C.D. (1977) Biology of the range crane fly, *Tipula simplex* Doane. *Pan-Pacific Entomologist* 53, 118–123.

Harvey, G.T. (1985) Egg weight as a factor in the overwintering survival of spruce budworm (Lepidoptera: Tortricidae) larvae. *The Canadian Entomologist* 117, 1451–1461.

Harvey, G.T. (1996) Population genetics of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae), in relation to geographical and population density differences. *The Canadian Entomologist* 128, 219–243.

Harvey, J.A., Van Nouhuys, S. *et al.* (2005) Effects of quantitative variation in allelochemicals in Plantago lanceolata on development of a generalist and a specialist herbivore and their endoparasitoids. *Journal of Chemical Ecology* 31, 287–302.

Harvey, J.A., Gols, R. *et al.* (2015) Host preference and offspring performance are linked in three congeneric hyperparasitoid species. *Ecological Entomology* 40, 114–122.

Hassanali, A., Njagi, P.G.N. *et al.* (2005) Chemical ecology of locusts and related acridids. *Annual Review of Entomology* 50, 223–245.

Hassall, C., Sherratt, T.N. *et al.* (2015) Live fast, die old: no evidence for reproductive senescence or costs of mating in a damselfly (Odonata: Zygoptera). *Journal of Animal Ecology* 84, 1542–1554.

Hassell, M.P. (1966) Evaluation of parasite or predator responses. *Journal of Animal Ecology* 35, 65–76.

Hassell, M.P. (1968) The behavioural response of a tachinid fly (*Cyzenis albicans* (Fall.)), to its host the winter moth (*Operophtera brumata* (L.)). *Journal of Animal Ecology* 37, 627–639.

Hassell, M.P. (1969) A study of the mortality factors acting upon *Cyzenis albicans* (Fall.), a tachinid parasite of the winter moth (*Operophtera brumata* (L.)). *Journal of Animal Ecology* 38, 329–339.

Hassell, M.P. (1975) Density dependence in single species populations. *Journal of Animal Ecology* 44, 283–295.

Hassell, M.P. (1978) *The Dynamics of Arthropod Predator–Prey Systems*. Princeton, New Jersey, USA: Princeton University Press.

Hassell, M.P. (1980) Some consequences of habitat heterogeneity for population dynamics. *Oikos* 35, 150–160.

Hassell, M.P. (1982) What is searching efficiency? *Annals of Applied Biology* 101, 170–175.

Hassell, M.P. (1998a) *Insect Parasitoid Population Dynamics*. Oxford, UK: Oxford University Press.

Hassell, M.P. (1998b) The regulation of populations by density-dependent processes. In: Dempster, J.P. and McLean, I.F.G. (eds) (1998) *Insect Populations in Theory and Practice*. Dordrecht, Germany: Kluwer Academic Publishers, pp. 29–51.

Hassell, M.P. (2000) *The Spatial and Temporal Dynamics of Insect Host-Parasitoid Interactions*. Oxford, UK: Oxford University Press.

Hassell, M.P. and May, R.M. (1986) Generalist and specialist natural enemies in insect predator-prey interactions. *Journal of Animal Ecology* 55, 923–940.

Hassell, M.P. and Southwood, T.R.E. (1978) Foraging strategies in insects. *Annual Review of Ecology and Systematics* 9, 75–98.

Hassell, M.P., Southwood, T.R.E. *et al*. (1987) The dynamics of the viburnum whitefly (*Aleurotrachelus jelinekii*): a case study of population regulation. *Journal of Animal Ecology* 56, 283–300.

Hassell, M.P., Latto, J. *et al*. (1989) Seeing the wood for the trees: detecting density dependence from existing life-table data. *Journal of Animal Ecology* 58, 883–892.

Hassell, M.P., Comins, H.N. *et al*. (1991) Spatial structure and chaos in insect population dynamics. *Nature* 353, 255–258.

Hassell, M.P., Comins, H.N. *et al*. (1994) Species coexistence and self-organising spatial dynamics. *Nature* 370, 290–292.

Hastings, A. and Harrison, S. (1994) Metapopulation dynamics and genetics. *Annual Review of Ecology and Systematics* 25,167–188.

Hastings, A. and Wolin, C.L. (1989) Within patch dynamics in a metapopulation. *Ecology* 70, 1261–1266.

Hastings, A., Hom, C.L. *et al*. (1993) Chaos in ecology: is Mother Nature a strange attractor? *Annual Review of Ecology and Systematics* 24, 1–33.

Hastings, I.M. (1994) Selfish DNA as a method of pest control. *Philosophical Transactions of the Royal Society B* 344, 313–324.

Hatcher, J. (2008) *The Black Death*. London, UK: Weidenfeld and Nicholson.

Hatcher, P.E. (1995) Three-way interactions between plant pathogenic fungi, herbivorous insects and their host plants. *Biological Reviews* 70, 639–694.

Haukioja, E. (1980) On the role of plant defences in the fluctuation of herbivore populations. *Oikos* 35, 202–213.

Haukioja, E. (1982) Are individuals really subordinated to their genes? A theory of living entities. *Journal of Theoretical Biology* 99, 357–375.

Haukioja, E. (1990) Induction of defenses in trees. *Annual Review of Entomology* 36, 25–42.

Haukioja, E. and Neuvonen, S. (1985) The relationship between size and reproductive potential in male and female *Epirrita autumnata* (Lep., Geometridae). *Ecological Entomology* 10, 267–270.

Hausmann, C., Mattiacci, L. *et al*. (2005) Role of host feeding niches and refuges in habitat-related behaviour of *Hyssopus pallidus* (Hymenoptera: Eulophidae), a larval parasitoid of the codling moth. *Bulletin of Entomological Research* 95, 429–436.

Havill, N.P. and Raffa, K.F. (2000) Compound effects of induced plant responses to insect herbivores and parasitoids: implications for tritrophic interactions. *Ecological Entomology* 25, 171–179.

Hawes, C., Begg, G.S. *et al*. (2005) Individuals as the basic accounting unit in studies of ecosystem function: functional diversity in shepherd's purse, *Capsella*. *Oikos* 109, 521–534.

Hawkins, B.A. (1990) Global patterns of parasitoid assemblage size. *Journal of Animal Ecology* 59, 57–72.

Hawkins, B.A. (1992) Parasitoid-host food webs and donor control. *Oikos* 65, 159–162.

Hawkins, B.A. and Cornell, H.V. (1994) Maximum parasitism rates and successful biological control. *Science* 266, 1886.

Hawkins, B.A. and Holyoak, M. (1998) Transcontinental crashes of insect populations? *The American Naturalist* 152, 480–484.

Hawkins, B.A. and Lawton, J.H. (1987) Species richness of parasitoids of British phytophagous insects. *Nature* 326, 788–790.

Hawkins, B.A., Askew, R.R. *et al.* (1990) Influences of host feeding-niche and food plant type on generalist and specialist parasitoids. *Ecological Entomology* 15, 275–280.

Hawkins, B.A., Cornell, H.V. *et al.* (1997) Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. *Ecology* 78, 2145–2152.

Hawkins, B.A., Mills, N.J. *et al.* (1999) Is the biological control of insects a natural phenomenon? *Oikos* 86, 493–506.

Hawkins, C.P. and MacMahon, J.A. (1989) Guilds: the multiple meaning of a concept. *Annual Review of Entomology* 34, 423–451.

Hazel, W., Ante, S. *et al.* (1998) The evolution of environmentally-cued pupal colour in swallowtail butterflies: natural selection for pupation site and pupal colour. *Ecological Entomology* 23, 41–44.

Heads, P.A. and Lawton, J.H. (1983) Studies on the natural enemy complex of the holly leaf miner: the effects of scale on the detection of aggregative responses and the implications for biological control. *Oikos* 40, 267–276.

Healy, T.P. and Jepson, P.C. (1988) The location of floral nectar sources by mosquitoes: the long-range responses of *Anopheles arabiensis* Patton (Diptera: Culicidae) to *Achillea millefolium* flowers and isolated floral odour. *Bulletin of Entomological Research* 78, 651–657.

Heathfield, D. and Russell, M. (1992) *Modern Economics*, 2nd edn. Hemel Hempstead, UK: Harvester Wheatsheaf.

Hebert, P.D.N. (1983) Egg dispersal patterns and adult feeding behaviour in the Lepidoptera. *The Canadian Entomologist* 115, 1477–1481.

Heg, D. and Rasa, O.A.E. (2004) Effects of parental body condition and size on reproductive success in a tenebrionid beetle with biparental care. *Ecological Entomology* 29, 410–419.

Heimpel, G.E. and Collier, T.R. (1996) The evolution of host-feeding behaviour in insect parasitoids. *Biological Reviews* 71, 373–400.

Heinrich, B. (1975) Energetics of pollination. *Annual Review of Ecology and Systematics* 6, 139–170.

Heinrich, B. (1977) Why have some animals evolved to regulate a high body temperature? *The American Naturalist* 111, 623–640.

Heinrich, B. (1981) *Insect Thermoregulation*. New York, New York, USA: Wiley.

Heinrich, B. (1993) *The Hot-blooded Insects*. Berlin, Germany: Springer.

Heinrich, B. and Collins, S.L. (1983) Caterpillar leaf damage, and the game of hide-and-seek with birds. *Ecology* 64, 592–602.

Heinrich, B. and Mommsen, T.P. (1985) Flight of winter moths near 0°C. *Science* 228, 177–179.

Heinrichs, E.A. and Mochida, A. (1984) From secondary to major pest status: the case of insecticide-induced rice brown planthopper, *Nilaparvata lugens*, resurgence. *Protection Ecology* 7, 201–218.

Heisswolf, A., Klemola, T. *et al.* (2009) Shifting body weight-fecundity relationship in a capital breeder: maternal effects on egg numbers of the autumnal moth under field conditions. *Bulletin of Entomological Research* 99, 73–81.

Henderson, I.F. and Clements, R.O. (1979) Differential susceptibility to pest damage in agricultural grasses. *Journal of Agricultural Science* 93, 465–472.

Hengeveld, R. and Haeck, J. (1982) The distribution of abundance. 1. Measurements. *Journal of Biogeography* 9, 303–316.

Henneman, M.L. and Memmott, J. (2001) Infiltration of a Hawaiian community by introduced biological control agents. *Science* 293, 1314–1316.

Henson, W.R. (1951) Mass flights of spruce budworm. *The Canadian Entomologist* 83, 240.

Herbert, K.S., Umina, P.A. *et al.* (2010) Clone lineages of grape phylloxera differ in their performance on *Vitis vinifera*. *Bulletin of Entomological Research* 100, 671–678.

Hering, E.M. (1951) *Biology of the Leaf Miners*. The Netherlands: Junk.

Herms, D.A. and Mattson, W.J. (1992) The dilemma of plants: to grow or defend. *The Quarterly Review of Biology* 67, 283–335.

Herrel, N. and Amerasinghe, F.P. (2004) Adult anopheline ecology and malaria transmission in irrigated areas of South Punjab, Pakistan. *Medical and Veterinary Entomology* 18, 141–152.

Hespenheide, H. (1973) A novel mimicry complex: beetles and flies. *Journal of Entomology* 48, 49–56.

Hespenheide, H. (1991) Bionomics of leaf miners. *Annual Review of Entomology* 36, 535–560.

Hewitt, G. (2000) The genetic legacy of the Quaternary ice ages. *Nature* 405, 907–913.

Hickey, W.A. and Craig, G.B. (1966) Genetic distortion of sex ratio in the mosquito *Aedes aegypti*. *Genetics* 53, 1177–1196.

Hickling, R., Roy, D.B. *et al.* (2005) A northward shift of range margins in British Odonata. *Global Change Biology* 11, 502–506.

Hickling, R., Roy, D.B. *et al.* (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12, 450–455.

Hicks, B.J., Barbour, D.A. *et al.* (2001) The history and control of the pine beauty moth, *Panolis flammea* (D. & S.) (Lepidoptera: Noctuidae), in Scotland from 1976 to 2000. *Agricultural and Forest Entomology* 3, 161–168.

Higashiura, Y. (1987) Larval densities and a life-table for the gypsy moth, *Lymantria dispar*, estimated using the head capsule collection method. *Ecological Entomology* 12, 25–30.

Higashiura, Y. (1989) Survival of eggs in the gypsy moth *Lymantria dispar*. 1. Predation by birds. *Journal of Animal Ecology* 58, 403–412.

Hightower, B.G., Adams, A.L. *et al.* (1965) Dispersal of released irradiated laboratory-reared screw-worm flies. *Journal of Economic Entomology* 58, 373–374.

Hiiesaar, K., Williams, I. *et al.* (2009) Factors affecting cold hardiness in the small striped flea beetle, *Phyllotreta undulata*. *Entomologia Experimentalis et Applicata* 131, 278–285.

Hildebrand, J.G. (1995) Analysis of chemical signals by nervous systems. *Proceedings of the National Academy of Sciences USA* 92, 67–74.

Hilker, M. and Meiners, T. (2006) Early herbivore alert: insect eggs induce plant defense. *Journal of Chemical Ecology* 32, 1379–1397.

Hill, D.S. (1983) *Agricultural Insect Pests of the Tropics and their Control*, 2nd edn. Cambridge, UK: Cambridge University Press.

Hill, D.S. (1997) *The Economic Importance of Insects*. London, UK: Chapman and Hall.

Hill, J.K., Thomas, C.D. *et al.* (1996) Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *Journal of Animal Ecology* 65, 725–735.

Hinnebusch, B.J., Rudolf, A.E. *et al.* (2002) Role of Yersinia murine toxin in survival of *Yersinia pestis* in the midgut of the flea vector. *Science* 296, 733–735.

Hinton, H.E. (1946) Concealed phases in the metamorphosis of insects. *Nature* 157, 552–553.

Hinton, H.E. (1969) Respiratory systems of insect egg shells. *Annual Review of Entomology* 14, 343–368.

Hinton, H.E. (1973) Natural deception. In:. Gregory, R.L and Gombrich, E.H. (eds) *Illusion in Nature and Art*. New York, New York, USA: Scribners, pp. 96–159.

Hinton, H.E. (1977) Subsocial behaviour and biology of some Mexican membracid bugs. *Ecological Entomology* 2, 61–79.

Hinton, H.E. (1981) *Biology of Insect Eggs*. Oxford, UK: Pergamon Press.

Hirschberger, P. (1999) Larval population density affects female weight and fecundity in the dung beetle *Aphodius ater*. *Ecological Entomology* 24, 316–322.

Hirzel, A.H., Nisbet, R.M. *et al.* (2007) Host-parasitoid spatial dynamics in heterogeneous landscapes. *Oikos* 116, 2082–2096.

Hoballah, M.E., Degen, T. *et al.* (2004) Occurrence and direct control potential of parasitoids and predators of the fall army worm (Lepidoptera: Noctuidae) on maize in the subtropical lowlands of Mexico. *Agricultural and Forest Entomology* 6, 83–88.

Hobbs, M.R., Venkatachalam, U. *et al.* (2002) A new NOS2 promoter polymorphism associated with increased nitric oxide production and protection from severe malaria in Tanzanian and Kenyan children. *The Lancet* 360, 1468–1475.

Hochberg, M.E. and Waage, J.K. (1991). A model for the biological control of *Oryctes rhinoceros* (Coleoptera: Scarabaeidae) by means of pathogens. *Journal of Applied Ecology* 28, 514–541.

Hocking, B. (1952) Autolysis of flight muscles in a mosquito. *Nature* 169, 1101.

Hoddle, M.S., Van Driesche, R.G. *et al.* (1998) Biology and use of the whitefly parasitoid *Encarsia formosa*. *Annual Review of Entomology* 43, 645–669.

Hodĕk, A. (1993) Intraspecific variation in body size and fecundity in insects. *Oikos* 66, 483–492.

Hodek, I. (2012) Diapause/dormancy. In: Hodek, I., van Emden, H.F. *et al.* (eds) *Ecology and Behaviour of the Ladybird Beetles*. Oxford, UK: Blackwell.

Hodek, I. and Honĕk, A. (1996) *Ecology of the Coccinellidae*. Dordrecht, Germany: Kluwer Academic Publishers.

Hodek, I., van Emden, H.F. *et al.* (eds) (2012) *Ecology and Behaviour of the Ladybird Beetles*. Oxford, UK: Blackwell.

Hodkinson, I.D. (1997) Progressive restriction of host plant exploitation along a climatic gradient: the willow psyllid *Cacopsylla groenlandica* in Greenland. *Ecological Entomology* 22, 47–54.

Hoffmann, A.A. and Blows, M.W. (1994) Species borders: ecological and evolutionary perspectives. *Trends in Ecology and Evolution* 9, 223–227.

Hoffmann, A.A., Reynolds, K.T. *et al*. (2008) A high incidence of parthenogenesis in agricultural pests. *Proceedings of the Royal Society B* 275, 2473–2481.

Hoffmeister, T.S. and Gienapp, P. (2001) Discrimination against previously searched, host-free patches by a parasitoid foraging for concealed hosts. *Ecological Entomology* 26, 487–494.

Hogg, J.C. and Hurd, H. (1997) The effects of natural *Plasmodium falciparum* infection on the fecundity and mortality of *Anopheles gambiae* s.l. in north east Tanzania. *Parasitology* 114, 325–331.

Hokkanen, H.M.T. (1991) Trap cropping in pest management. *Annual Review of Entomology* 36, 119–138.

Hokkanen, H.M.T. and Pimentel, D. (1989) New associations in biological control: theory and practice. *The Canadian Entomologist* 121, 829–840.

Holdaway, F.G. (1932) An experimental study of the growth of populations of the flour beetle, *Tribolium confusum* Duval, as affected by atmospheric moisture. *Ecological Monographs* 2, 262–304.

Holden, C. (1996) Ebola: ancient history of “new” disease. *Science* 272, 1591.

Holland, J.M. (ed.) (2002) *The Agroecology of Carabid Beetles*. Andover, UK: Intercept.

Holland, J.N. and Fleming, T.H. (1999) Mutualistic interactions between *Upiga virescens* (Pyralidae), a pollinating seed-consumer, and *Lophocereus schottii* (Cactaceae). *Ecology* 80, 2074–2084.

Holland, J.N., Chamberlain, S.A. *et al*. (2009) Optimal defence theory predicts investment in extrafloral nectar resources in an ant-plant mutualism. *Journal of Ecology* 97, 89–96.

Hollande, M.A.-C. (1920) Oenocytoides et tératocytes du sang des chenilles. *Compte Rendu de l’Academie des Sciences, Paris* 170, 1341–1344.

Hölldobler, B. and Wilson, E.O. (1990) *The Ants*. Berlin, Germany: Springer.

Holliday, N.J. (1977) Population ecology of winter moths (*Operophtera brumata*) on apple in relation to larval dispersal and time of bud burst. *Journal of Applied Ecology* 14, 803–813.

Holliday, N.J. (1985) Maintenance of the phenology of the winter moth. *Biological Journal of the Linnean Society* 25, 221–234.

Holling, C.S. (1959a) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist* 91, 293–320.

Holling, C.S. (1959b) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* 91, 385–398.

Holling, C.S. (1973) Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4, 1–23.

Holling, C.S. (1992) Cross-scale morphology, geometry and dynamics of ecosystems. *Ecological Monographs* 62, 447–502.

Holmes, N.D. (1982) Population dynamics of the wheat stem sawfly, *Cephus cinctus* (Hymenoptera: Cephidae), in wheat. *The Canadian Entomologist* 114, 775–788.

Holopainen, J.K. and Peltonen, P. (2002) Bright autumn colours of deciduous trees attract aphids: nutrient retranslocation hypothesis. *Oikos* 99, 184–188.

Holt, R.D. (1977) Predation, apparent competition and the structure of prey communities. *Theoretical Population Biology* 12, 197–229.

Holt, R.D. (1984) Spatial heterogeneity, indirect interactions and the coexistence of prey species. *The American Naturalist* 124, 377–406.

Holt, R.D. and Barfield, M. (2009) Trophic interactions and range limits: the diverse roles of predation. *Proceedings of the Royal Society B* 276, 1435–1442.

Holt, R.D. and Lawton, J.H. (1994) Ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics* 25, 459–520.

Honěk, A. (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* 66, 483–492.

Hood, G.R., Egan, S.P. *et al*. (2012) Evidence for sexual isolation as a prezygotic barrier to gene flow between morphologically divergent species of *Rhagoletis* fruit flies. *Ecological Entomology* 37, 521–528.

Hooper, L.R.E., Dixon, P.L. *et al*. (2002) Distribution and seasonal activity of adult carrot rust flies (Diptera: Psilidae). *The Canadian Entomologist* 134, 703–706.

Hopper, K.R. (1999) Risk-spreading and bet-hedging in insect population biology. *Annual Review of Entomology* 44, 535–560.

Horn, H.S. (1971) *The Adaptive Geometry of Trees*. Princeton, New Jersey, USA: Princeton University Press.

Horsfield, A., Sallam, M.N.S. *et al.* (2008) Role of climatic factors on damage incidence by *Dermolepida albohirtum* (Coleoptera: Scarabaeidae), in Burdekin sugarcane fields, Australia. *Journal of Economic Entomology* 101, 334–340.

Hoskins, W.G. (1955) *The Making of the English Landscape*. London, UK: Hodder and Stoughton.

Hotez, P.J., Alvarado, M., *et al.* (2014) The Global Burden of Disease Study 2010: Interpretation and implications for the neglected tropical diseases. *PLoS Neglected Tropical Diseases* 8, e2865.

Houle, D. (1992) Comparing evolvability and variability of quantitative traits. *Genetics* 130, 195–204.

Howard, F.W. (1995) Reduction of damage to mahogany by mahogany shoot borer and mahogany leaf miner by use of azadirachtin. *Journal of Tropical Forest Science* 7, 454–461.

Howard, L.O. (1910) On the habit with certain Chalcidoidea of feeding at puncture holes made by the ovipositor. *Journal of Economic Entomology* 3, 257–260.

Howard, L.O. (1931) *The Insect Menace*. New York, New York, USA: Century Press.

Howard, L.O. and Fiske, W.F. (1911) The importation into the United States of the parasites of the gypsy moth and brown-tail moth. *United States Bureau of Entomology Bulletin* 91, 1–344.

Howarth, F.G. (1991) Environmental impacts of classical biological control. *Annual Review of Entomology* 36, 485–509.

Howe, G.A. and Jander, G. (2008) Plant immunity to insect herbivores. *Annual Review of Plant Biology* 59, 41–66.

Howling, G.G., Bale, J.S., *et al.* (1994) Effects of extended and repeated exposures to low temperature on mortality of the peach potato aphid *Myzus persicae*. *Ecological Entomology* 19, 361–366.

Hsu, C.L., Agnello, A.M. *et al.* (2009) Edge effects in the directionally biased distribution of *Choristoneura rosaceana* (Lepidoptera: Tortricidae) in apple orchards. *Environmental Entomology* 38, 433–441.

Huang, X. and Renwick, J.A.A. (1993) Differential selection of host plants by two *Pieris* species: the role of oviposition stimulants and deterrents. *Entomologia Experimentalis et Applicata* 68, 59–69.

Huang, X., Vergne, E. *et al.* (1992) Failure of dengue viruses to replicate in *Culex quinquefasciatus* (Diptera: Culicidae). *Journal of Medical Entomology* 29, 911–914.

Hudon, M. and LeRoux, E.J. (1961) Variation between samples of different stages, and of mortalities from some factors, of the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae) on sweet corn in Quebec. *The Canadian Entomologist* 93, 867–888.

Huffaker, C.B. (1971) (ed.) *Biological Control*. New York, New York, USA: Plenum Press.

Huffaker, C.B. and Kennett, C.E. (1966) Studies of two parasites of olive scale, *Parlatoria oleae* (Colvee). 1V. Biological control of *Parlatoria oleae* (Colvee) through the compensatory action of two introduced parasites. *Hilgardia* 37, 283–335.

Huffaker, C.B. and Kennett, C.E. (1969) Some aspects of assessing efficiency of natural enemies. *The Canadian Entomologist* 101, 425–447.

Huffaker, C.B. and Messenger, P.S. (1964) The concept and significance of natural control. In: Debach, P. (ed.) *Biological Control of Pests and Weeds*. London, UK: Chapman and Hall, pp. 74–117.

Huffaker, C.B. and Messenger, P.S. (1976) (eds). *Theory and Practice of Biological Control*. New York, New York, USA: Academic Press.

Huffaker, C.B. and Rabb, R.L. (1984) *Ecological Entomology*. New York, New York, USA: Wiley.

Hughes, R.D. (1963) Population dynamics of the cabbage aphid, *Brevicoryne brassicae* (L.). *The Journal of Animal Ecology* 32, 393–424.

Hughes, R.D. and Mitchell, B. (1960) The natural mortality of *Erioischia brassicae* (Bouché) (Dipt., Anthomyiidae): life tables and their interpretation. *Journal of Animal Ecology* 29, 359–374.

Hughes, R.G. (1986) Theories and models of species abundance. *The American Naturalist* 128, 879–899.

Hulbe, C.L., Douglas, R. *et al.* (2004) Catastrophic ice shelf break-up as the source of Heinrich event icebergs. *Paleoceanography* 19, 15.

Hull, D.L. (1997) The ideal species concept – and why we can't get it. In: Claridge, M.F. *et al.* (ed.) *Species: the Units of Biodiversity*. London, UK: Chapman and Hall, pp. 357–380.

Hull, F.M. (1962) *Robber Flies of the World*. Bulletin 224, part 1. Washington, DC, USA: Smithsonian Institute of Washington.

Hunt, D.W.A. and Tan, C.S. (2000) Overwintering densities and survival of the Colorado potato beetle (Coleoptera: Chrysomelidae) in and around tomato (Solanaceae) fields. *The Canadian Entomologist* 132, 103–105.

Hunt, R.H., Coetzee, M. *et al*. (1998) The *Anopheles gambiae* complex: a new species from Ethiopia. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 92, 231–235.

Hunter, A.F. (1991) Traits that distinguish outbreaking and non-outbreaking Macrolepidoptera feeding on northern hardwood trees. *Oikos* 60, 275–282.

Hunter, A.F. (1995) The ecology and evolution of reduced wings in forest Macrolepidoptera. *Evolutionary Ecology* 9, 275–287.

Hunter, M.D. (1998) Interactions between *Operophtera brumata* and *Tortrix viridana* on oak: new evidence from time-series analysis. *Ecological Entomology* 23, 168–173.

Hunter, M.D., Watt, A.D. *et al*. (1991) Outbreaks of the winter moth on Sitka spruce in Scotland are not influenced by nutrient deficiencies of trees, tree budburst or pupal predation. *Oecologia* 86, 62–69.

Hunter, M.D., Varley, G.C. *et al*. (1997) Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. *Proceedings of the National Academy of Sciences USA* 94, 9176–9181.

Hurd, H. (2003) Manipulation of medically important insect vectors by their parasites. *Annual Review of Entomology* 48, 141–161.

Huston, M.A. (1993) Biological diversity, soils and economics. *Science* 262, 1676–1680.

Huston, M.A. (1994) *Biological Diversity: the Co-existence of Species on Changing Landscapes*. Cambridge, UK: Cambridge University Press.

Hutchinson, G.E. (1953) The concept of pattern in ecology. *Proceedings of the Academy of Natural Sciences of Philadelphia* 105, 1–12.

Hutchinson, G.E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* 93, 145–159.

Hutchinson, K.J. and King, K.L. (1980) The effects of sheep stocking levels on invertebrate abundance, biomass, and energy utilisation in a temperate sown grassland. *Journal of Applied Ecology* 17, 369–387.

Hutchison, D.W. and Templeton, A.R. (1999) Correlation of pairwise genetic and geographical distance measures: inferring the relative influences of gene flow and drift on the distribution of genetic diversity. *Evolution* 53, 1898–1914.

Huth, W. (2000) Viruses of the Gramineae in Germany – a short review. *Journal of Plant Diseases and Protection* 107, 406–414.

Hutt, H.J., van Emden, H.F. *et al*. (1994) Stimulation of plant growth and aphid populations by a formulation ingredient of “Cymbush” (cypermethrin). *Bulletin of Entomological Research* 84, 509–513.

Huxel, G.R. and Hastings, A. (1998) Population size dependence, competitive coexistence and habitat destruction. *Journal of Animal Ecology* 67, 446–453.

Huxley, C.R. and Cutler, D.F. (1991) (eds) *Ant–Plant Interactions*. Oxford, UK: Oxford University Press.

Huxley, J.S. (1938) Clines: an auxiliary taxonomic principle. *Nature* 142, 219–220.

Huxley, J.S. (1942) *Evolution: the Modern Synthesis*. London, UK: Allen and Unwin.

Ibrahim, K.M. (2001) Plague dynamics and population genetics of the desert locust: can turnover during recession maintain population genetic structure? *Molecular Ecology* 10, 581–591.

Idris, A.B. and Grafius, E. (1996) Effects of wild and cultivated host plants on oviposition, survival, and development of diamondback moth (Lepidoptera: Plutellidae) and its parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae). *Environmental Entomology* 25, 825–833.

Ikawa, T. and Okabe, H. (1985) Regulation of egg number per host to maximise the reproductive success in the gregarious parasitoid, *Apanteles glomeratus* L. (Hymenoptera: Braconidae). *Applied Entomology and Zoology* 20, 331–339.

Inbar, M. and Gerling, D. (2008) Plant-mediated interactions between whiteflies, herbivores, and natural enemies. *Annual Review of Entomology* 53, 431–448.

Inghe, O. and Tamm, C.O. (1985) Survival and flowering of perennial herbs. 4. *Oikos* 45, 400–420.

Innocent, T.M., West, S.A. *et al*. (2011) Lethal combat over limited resources: testing the importance of competitors and kin. *Behavioural Ecology* 22, 923–931.

Iranipour, S., Kharrazi Pakdel, A. *et al.* (2011) Life tables for sunn pest, *Eurygaster integriceps* (Heteroptera: Scutelleridae) in northern Iran. *Bulletin of Entomological Research* 101, 33–44.

Isaacs, R. and Byrne, D.N. (1998) Aerial distribution, flight behaviour, and egg load: their inter-relationship during dispersal by the sweet potato whitefly. *Journal of Animal Ecology* 67, 741–750.

Ito, F. and Higashi, S, (1991) Variance of ant effects on the different life forms of moth caterpillars. *Journal of Animal Ecology* 60, 327–334.

Ito, J., Ghosh, A. *et al.* (2002) Transgenic anopheline mosquitoes impaired in transmission of a malarial parasite. *Nature* 417, 452–455.

Ito, Y. and Miyashita, K. (1968) Biology of *Hyphantria cunea* Drury (Lepidoptera: Arctiidae) in Japan. Preliminary life tables and mortality data in urban areas. *Researches on Population Ecology* 10, 177–209.

Ittyeipe, K. and Taffe, C.A. (1982) The biology and population dynamics of *Monobia mochii* Soika, a rare, solitary eumenid in Jamaica. *Caribbean Journal of Science* 17, 45–58.

Ives, A.R. (1991) Chaos in time and space. *Nature* 353, 214–215.

Ives, A.R. (1996) Evolution of insect resistance to *Bacillus thuringiensis*-transformed plants. *Science* 273, 1412–1413.

Ives, A.R. and Settle, W.H. (1996) The failure of a parasitoid to persist with a superabundant host: the importance of the numerical response. *Oikos* 75, 269–278.

Ives, A.R. and Settle, W.H. (1997) Metapopulation dynamics and pest control in agricultural systems. *The American Naturalist* 149, 220–246.

Ives, W.G.H. (1976) The dynamics of larch sawfly (Hymenoptera: Tenthredinidae) populations in southwestern Manitoba. *The Canadian Entomologist* 108, 701–730.

Iwanga, K. and Tojo, S. (1986) Effects of juvenile hormone and rearing density on wing dimorphism and oocyte development in the brown planthopper, *Nilaparvata lugens*. *Journal of Insect Physiology* 32, 585–590.

Iwata, K. (1955) The comparative anatomy of the ovary in Hymenoptera. Part 1. Aculeata. *Mushi* 29, 17–36.

Jackson, C.H.N. (1949) The biology of tsetse flies. *Biological Reviews* 24, 174–199.

Jackson, D.A. and Somers, K.M. (1991) The spectre of “spurious” correlations. *Oecologia* 86, 147–151.

Jackson, D.J. (1920) Bionomics of weevils of the genus *Sitones* injurious to leguminous crops in Britain. *Annals of Applied Biology* 7, 269–298.

Jackson, D.J. (1928) The inheritance of long and short wings in the weevil, *Sitona hispidula*, with a discussion of wing reduction among beetles. *Transactions of the Royal Society of Edinburgh* 55, 665–735.

Jackson, D.J. (1958) Observations on the biology of *Caraphractus cintus* Walker (Hymenoptera: Mymaridae), a parasitoid of the eggs of Dytiscidae. *Transactions of the Royal Entomological Society of London* 110, 533–554.

Jackson, H.B., Baum, K.A. *et al.* (2009) habitat-specific movement and edge-mediated behavior of the saproxylic insect *Odontotaenius disjunctus* (Coleoptera: Passalidae). *Environmental Entomology* 38, 1411–1422.

Jackson, R.B., Manwaring, J.H. *et al.* (1990) Rapid physiological adjustment of roots to localised soil enrichment. *Nature* 344, 58–60.

Jacques, R.P., Hardman, J.M. *et al.* (1994) Orchard trials in Canada on control of *Cydia pomonella* (Lepidoptera: Tortricidae) by granulosis virus. *Entomophaga* 39, 281–292.

Jaenike, J. (1978) On optimal oviposition behaviour in phytophagous insects. *Theories in Population Biology* 14, 350–356.

Jaenike, J. (1981) Criteria for ascertaining the existence of host races. *The American Naturalist* 117, 830–834.

Jaksic, F.M. (1981) Abuse and misuse of the term “guild” in ecological studies. *Oikos* 37, 397–400.

James, D.G. (1987) Effects of temperature and photoperiod on the development of *Vanessa kershawi* McCoy and *Junonia villida* Godart (Lepidoptera: Nymphalidae*)*. *Journal of the Australian Entomological Society* 26, 289–292.

Jang, E.B., Casana-Giner, V. *et al.* (2007) Field captures of wild melon fly (Diptera: Tephritidae) with an improved male attractant, raspberry ketone formate. *Journal of Economic Entomology* 100, 1124–1128.

Jansen, V.A.A., Turelli, M. *et al.* (2008) Stochastic spread of *Wolbachia*. *Proceedings of the Royal Society B* 275, 2769–2776.

Janzen, D.H. (1966) Coevolution of mutualism between ants and acacias in Central America. *Evolution* 20, 249–275.

Janzen, D.H. (1968) Host plants as islands in evolutionary and contemporary time. *The American Naturalist* 102, 592–595.

Janzen, D.H. (1970) Herbivores and the number of tree species in tropical rain forests. *The American Naturalist* 104, 501–528.

Janzen, D.H. (1971) Euglossine bees as long-distance pollinators of tropical plants. *Science* 171, 203–205.

Janzen, D.H. (1980) When is it coevolution? *Evolution* 34, 611–612.

Janzen, D.H. (1981) Patterns of herbivory in a tropical deciduous forest. *Biotropica* 13, 271–282.

Janzen, D.H. (1984) Two ways to be a tropical big moth: Santa Rosa Saturnids and Sphingids. *Oxford Surveys in Evolutionary Biology* 1, 85–140.

Janzen, D.H. (1988) On the broadening of insect-plant research. *Ecology* 69, 905.

Jaramillo, J., Borgemeister, C. *et al.* (2006) Coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae): searching for sustainable control strategies. *Bulletin of Entomological Research* 96, 223–233.

Jauker, F. and Wolters, V. (2008) Hover flies are efficient pollinators of oilseed rape. *Oecologia* 156, 819–823.

Jaworska, M. and Wiech, K. (1988) Susceptibility of the clover root weevil, *Sitona hispidulus* F. (Col., Curculionidae) to *Steinernema feltiae*, *S. bibionis*, and *Heterorhabditis bacteriophora*. *Journal of Applied Entomology* 106, 372–376.

Jayasingh, D.B. and Freeman, B.E. (1977) Trap-nesting solitary aculeates (Insecta: Hymenoptera) in St. Catherine, Jamaica. *Caribbean Journal of Science* 13, 69–78.

Jayasingh, D.B. and Freeman, B.E. (1980) The comparative population dynamics of eight solitary bees and wasps (Aculeata; Apocrita; Hymenoptera) trap-nested in Jamaica. *Biotropica* 12, 214–219.

Jefferies, R.L. and Maron, J.L. (1997) The embarrassment of riches: atmospheric deposition of nitrogen and community and ecosystem processes. *Trends in Ecology and Evolution* 12, 74–78.

Jeffries, M.J. and Lawton, J.H. (1984) Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society* 23, 269–286.

Jennions, M.D., Petrie, M. (2000) Why do females mate multiply? A review of the genetic benefits. *Biological Reviews Cambridge Philosophical Society* 75, 21–64.

Jepson, W.F. and Heard, A.J. (1959) The frit fly and other stem-boring Diptera in winter wheat and host grasses. *Annals of Applied Biology* 47, 114–130.

Jermy, T. (1984) Evolution of insect/host plant relationships. *The American Naturalist* 124, 609–630.

Jermy, T., Hanson, F.E. *et al.* (1968) Induction of specific food preferences in lepidopterous larvae. *Entomologia Experimentalis et Applicata* 11, 211–230.

Jervis, M.A. and Kidd, N.A.C. (1986) Host-feeding strategies in hymenopteran parasitoids. *Biological Reviews* 61, 395–434.

Jervis, M.A. and Kidd, N.A.C. (1991) The dynamic significance of host-feeding by insect parasitoids: what modellers ought to consider. *Oikos* 62, 97–99.

Jervis, M.A., Heimpel, G.E. *et al.* (2001) Life-history strategies in parasitoid wasps: a comparative analysis of “ovigeny”. *Journal of Animal Ecology* 70, 442–458.

Jervis, M.A., Ellers, J. *et al.* (2008) Resource acquisition, allocation and utilization in parasitoid reproductive strategies. *Annual Review of Entomology* 53, 361–385.

Jing, K-H., and Kang, L. (2003) Geographical variation in egg cold hardiness: a study on the adaptation strategies of the migratory locust *Locusta migratoria* L. *Ecological Entomology* 28, 151–158.

Joern, A. and Lawlor, L.R. (1980) Food and microhabitat utilization by grasshoppers from arid grasslands: comparisons with neutral models. *Ecology* 61, 591–599.

Johannesen, J., Lux, B. *et al.* (2008) Invasion biology and host specificity of the grapevine yellows disease vector *Hyalesthes obsoletus* in Europe. *Entomologia Experimentalis et Applicata* 126, 217–227.

Johns, R., Quiring, D.T. *et al.* (2009) Foliage-age mixing within balsam fir increases the fitness of a generalist caterpillar. *Ecological Entomology* 34, 624–631.

Johnson, B. (1966) Wing polymorphism in aphids III. The influence of the host plant. *Entomologia Experimentalis et Applicata* 9, 213–222.

Johnson, C.G. (1940) The longevity of the fasting bed bug (*C. lectularius* L.) under experimental conditions and particularly in relation to the saturation deficit law of water loss. *Parasitology* 32, 239–270.

Johnson, C.G. (1960) The basis for a general system of insect migration and dispersal by flight. *Nature* 186, 348–350.

Johnson, C.G. (1969) *Migration and Dispersal of Insects by Flight*. London, UK: Methuen.

Johnson, C.G., Southwood, T.R.E. *et al.* (1957) A new method for extracting arthropods and molluscs from grassland and herbage with a suction apparatus. *Bulletin of Entomological Research* 48, 211–218.

Johnson, C.G., Taylor, L.R. *et al.* (1962) High altitude migration of *Oscinella frit* L. (Diptera: Chloropidae). *Journal of Animal Ecology* 31, 373–383.

Johnson, K.J.R. (1984) Identification of *Eoreuma loftini* (Dyar) (Lepidoptera: Pyralidae) in Texas, 1980: forerunner of other sugarcane boring pest immigrants from Mexico? *Bulletin of the Entomological Society of America* 30, 47–52.

Johnson, M.T. (1997) Interaction of resistant plants and wasp parasitoids of tobacco budworm. *Environmental Entomology* 26, 207–214.

Johnson, S.J. (1995) Insect migration in North America: synoptic-scale transport in a highly seasonal environment. In: Drake, V.A. and Gatehouse, A.G. (eds) *Insect Migration: Tracking Resources Through Space and Time*. Cambridge, UK: Cambridge University Press, pp. 31–66.

Johnston, J.S. and Heed, W.B. (1976) Dispersal of desert-adapted *Drosophila*: the saguaro-breeding *D. nigrospiracula*. *The American Naturalist* 110, 629–651.

Jolivet, P. and Petitpierre, E. (1976) Les plant-hôtes connues des Chrysolina (Col. Chrysomelidae). Essai sur les types de sélection trophique. *Annales - Société Entomologique de France* 12, 123–149.

Jolly, G.M. (1965) Explicit estimates from capture-recapture data with both death and immigration – stochastic model. *Biometrika* 52, 225–247.

Jones, A.G., Arnold, S.J. *et al.* (2007) The mutation matrix and the evolution of evolvability. *Evolution* 61, 727–745.

Jones, C.G., Lawton, J.H. *et al.* (1994) Organisms as ecosystem engineers. *Oikos* 69, 373–386.

Jones, C.G., Lawton, J.H. *et al.* (1997) Positive and negative effects of organisms as ecosystem engineers. *Ecology* 78, 1946–1957.

Jones, D.A. (1979) Chemical defense: primary or secondary function? *The American Naturalist* 113, 445–451.

Jones, F.G.W. and Jones, M.G. (1984) *Pests of Field Crops*, 3rd edn. London, UK: Arnold.

Jones, J.S. (1999) *Almost Like a Whale*. London, UK: Transworld.

Jones. M.G. (1976) The arthropod fauna of a winter wheat field. *The Journal of Applied Ecology* 13, 61–85.

Jones, R.E. (1977) Movement patterns and egg distribution in cabbage butterflies. *Journal of Animal Ecology* 46, 195–212.

Jones, R.E., Gilbert, N., *et al.* (1980) Long-distance movement of *Pieris rapae*. *Journal of Animal Ecology* 49, 629–642.

Jones, R.L. and Mitchell, J.F.B. (1991) Is water vapour understood? *Nature* 353, 210.

Jones, T.H., Hassell, M.P. *et al.* (1993) Spatial heterogeneity and the population dynamics of a host-parasitoid system. *Journal of Animal Ecology* 62, 251–262.

Joos, B. (1987) Carbohydrate use in the flight muscles of *Manduca sexta* during pre-flight warm-up. *The Journal of Experimental Biology* 133, 317–327.

Joos, B., Casey, T.M. *et al.* (1988) Roles of the tent in behavioral thermoregulation of eastern tent caterpillars. *Ecology* 69, 2004–2011.

Juliano, S.A. (1985) The effects of body size on mating and reproduction in *Brachinus lateralis* (Coleoptera: Carabidae). *Ecological Entomology* 10, 271–280.

Juliano, S.A. (1986) Food limitation of reproduction and survival for populations of *Brachinus* (Coleoptera: Carabidae). *Ecology* 67, 1036–1045.

Juliano, S.A. (1998) Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition? *Ecology* 79, 255–268.

Juliano, S.A. and Williams, F.M. (1985) On the evolution of handling time. *Evolution* 39, 212–215.

Jumean, Z., Rowland, E. *et al.* (2004) Male and female *Cydia pomonella* (Lepidoptera: Olethreutidae) larvae produce and respond to aggregation pheromone. *The Canadian Entomologist* 136, 871–873.

Kahn, D.M. and Cornell, H.V. (1983) Early leaf abscission and folivores: comments and considerations. *The American Naturalist* 122, 428–432.

Kaitala, V., Ranta, E. *et al.* (1996) Cyclic population dynamics and random perturbations. *Journal of Animal Ecology* 65, 249–251.

Kaitala V., Ranta, E. *et al.* (2001) Self-organised dynamics in spatially structured populations. *Proceedings of the Royal Society B* 268, 1655–1660.

Kalmus, H. (1944) Action of inert dusts on insects. *Nature* 153, 714–715.

Kalmus, H. (1945) Correlations between flight and vision, and particularly between wings and ocelli, in insects. *Proceedings of the Royal Entomological Society A* 20, 84–96.

Kalmus, H. (1960) *101 Simple Experiments with Insects*. New York, New York, USA: Doubleday.

Kaloshian, I. (2004) Gene-for-gene disease resistance: bridging insect pest and pathogen defence. *Journal of Chemical Ecology* 30, 2419–2438.

Kalshoven, L.G.E. (1953) Important outbreaks of insect pests in the forests of Indonesia. *Transactions of the 9th International Congress of Entomology* 2, 229–234.

Kalyebi, A., Overholt, W.A. *et al.* (2006) The effect of temperature and humidity on the bionomics of six African egg parasitoids (Hymenoptera: Trichogrammatidae). *Bulletin of Entomological Research* 96, 305–314.

Kammer, A. and Heinrich, B. (1978) Insect flight metabolism. *Advances in Insect Physiology* 13, 133–228.

Kankare, M., van Nouhuys, S. *et al.* (2005) Metapopulation genetic structure of two coexisting parasitoids of the Glanville fritillary butterfly. *Oecologia* 143, 77–84.

Kapatos, D.E. and Fletcher, B.S. (1986) Mortality factors and life-budgets for immature stages of the olive fly, *Dacus oleae* (Gmel.) (Diptera, Tephritidae), in Corfu. *Journal of Applied Entomology* 102, 326–342.

Karban, R. (1987) Herbivory dependent on plant age: a hypothesis based on acquired resistance. *Oikos* 48, 336–337.

Karban, R. and Baldwin, I.T. (1997) *Induced Responses to Herbivory*. Chicago, Illinois, USA: The University of Chicago Press.

Karban, R. and English-Loeb, G. (1997) Tachinid parasites affect host plant choice by caterpillars to increase caterpillar survival. *Ecology* 78, 603–611.

Karban, R. and Myers, J.H. (1989) Induced plant responses to herbivory. *Annual Review of Ecology and Systematics* 20, 331–348.

Karban, R., Karban, C. *et al.* (2010) Diet mixing enhances the performance of a generalist caterpillar, *Platyprepia virginalis*. *Ecological Entomology* 35, 92–99.

Karban, R., Grof-Tisza, P. *et al.* (2015) Caterpillars escape predation in habitat and thermal refuges. *Ecological Entomology* 40, 725–731.

Kareiva, P. (1987) Habitat fragmentation and the stability of predator-prey interactions. *Nature* 326, 388–390.

Karlsson, B. and Wiklund, C. (2005) Butterfly life history and temperature adaptations; dry open habitats select for increased fecundity and longevity. *Journal of Animal Ecology* 74, 99–104.

Kartohardjono, A. and Heinrichs, E.A. (1984) Population of the brown planthopper, *Nilaparvata lugens* (Stål.) (Homoptera: Delphacidae), and its predators on rice varieties with differing levels of resistance. *Environmental Entomology* 13, 359–365.

Kasule, F.K. (1991) Egg size increases with maternal age in the cotton stainer bugs *Dysdercus fasciatus* and *D. cardinalis* (Hemiptera: Pyrrhocoridae). *Ecological Entomology* 16, 345–349.

Kato, M. (1985) Life history and mortality pattern of the honeysuckle leaf-miner, *Phytomyza lonicerae* Robineau-Desboidy (Diptera, Agromyzidae). *Kontyu* 53, 604–615.

Katsoyannos, P., Kontodimas, D.C. *et al.* (1997) Summer diapause and winter quiescence of *Coccinella septempunctata* (Col. Coccinellidae) in central Greece. *Entomophaga* 42, 483–491.

Kauffman, S.A. (1993) *The Origins of Order*. Oxford, UK: Oxford University Press.

Kawai, A. (1978) Sibling cannibalism in the first instar larvae of *Harmonia axyridis* (Coleoptera: Coccinellidae). *Kontyu* 46, 14–19.

Kaya, H.K. and Gaugler, R. (1993) Entomopathogenic nematodes. *Annual Review of Entomology* 38, 181–206.

Keating, J., Mbogo, C.M. *et al.* (2005) *Anopheles gambiae* s.l. and *Anopheles funestus* mosquito distributions at 30 villages along the Kenyan coast. *Journal of Medical Entomology* 42, 241–246.

Keating, S.T. and Yendol, W.G. (1987) Influence of selected host plants on gypsy moth (Lepidoptera: Lymantriidae) larval mortality caused by a baculovirus. *Environmental Entomology* 16, 459–462.

Keddy, P.A. (2001) *Competition*. Dordrecht, Germany: Kluwer Academic Publications.

Keeling, M.J. and Rand, D.A. (1995) A spatial mechanism for the evolution and maintenance of sexual reproduction. *Oikos* 74, 414–424.

Keena, M.A., Cote, M.J. *et al.* (2008) World distribution of female flight and genetic variation in

Lymantria dispar (Lepidoptera: Lymantriidae). *Environmental Entomology* 37, 636–649.

Keil, S, Gu, H. *et al.* (2001) Response of *Cydia pomonella* to selection on mobility: laboratory evaluation and field verification. *Ecological Entomology* 26, 495–501.

Keith, S.A., Newton, A.C. *et al.* (2009) Taxonomic homogenisation of woodland plant communities over 70 years. *Proceedings of the Royal Society B* 276, 3539–3544.

Kelber, A. (1999) Ovipositing butterflies use a red receptor to see green. *The Journal of Experimental Biology* 202, 2619–2630.

Kelber, A. (2001) Receptor based models for spontaneous colour choices in flies and butterflies. *Entomologia Experimentalis et Applicata* 99, 231–244.

Kelber, A., Balkenius, A. *et al.* (2002) Scotopic colour vision in nocturnal hawk moths. *Nature* 419, 922–925.

Kendall, B.E., Bjornstad, O.N. *et al.* (2000) Dispersal, environmental correlation, and spatial synchrony in population dynamics. *The American Naturalist* 155, 628–636.

Kennedy, G.C. (2003) Tomato pests, parasitoids and predators: tritrophic interactions involving the genus *Lycopersicon*. *Annual Review of Entomology* 48, 51–72.

Kennedy, J.S. (1951) The migration of the Desert Locust (*Schistocerca gregaria* Forsk.) *Philosophical Transactions of the Royal Society B* 235, 163–290.

Kennedy, J.S. (1961a) Continuous polymorphism in locusts. In: *Insect Polymorphism*. *Symposium of the Royal Entomological Society of London* 1, 80–90.

Kennedy, J.S. (1961b) A turning point in the study of insect migration. *Nature* 189, 785–791.

Kennedy, J.S. (1967) Behaviour as physiology. In: Beament, J.W.L. and Treherne, J.E. (eds) *Insects and Physiology*. Edinburgh, UK: Oliver and Boyd.

Kennedy, J.S. (1983) Zigzagging and casting as a programmed response to wind-borne odour: a review. *Physiological Entomology* 8, 109–120.

Kennedy, J.S. and Booth, C.O. (1963a) Free flight of aphids in the laboratory. *The Journal of Experimental Biology* 40, 67–85.

Kennedy, J.S. and Booth, C.O. (1963b) Co-ordination of successive activities in an aphid. The effect of flight on the settling response. *The Journal of Experimental Biology* 40, 351–369.

Kennedy, P.C. and Wilson, L.F. (1971) Pine root collar damage to red pine plantations in Michigan related to host age, temperature, and stand location. *The Canadian Entomologist* 103, 1685–1690.

Kerr, R.A. (2000) A North Atlantic climate pacemaker for the centuries. *Science* 288, 1984–1986.

Kerslake, J.E. and Hartley, S.E. (1997) Phenology of winter moths feeding on common heather: effects of source population and manipulation of hatching dates. *Journal of Animal Ecology* 66, 375–385.

Kerswell, K.J. and Burd, M. (2012) Frequency-dependent and density-dependent larval competition between life-history strains of a fly, *Lucilia cuprina*. *Ecological Entomology* 37, 109–116.

Kessler, A. and Baldwin, I.T. (2001) Defensive function of herbivore-induced plant volatile emissions in nature. *Science* 291, 2141–2144.

Kettle, D.S. (1995) *Medical and Veterinary Entomology*, 2nd edn. Wallingford, UK: CAB International.

Kettlewell, H.B.D. (1973) *The Evolution of Melanism*. Oxford, UK: Clarendon Press.

Kevan, P.G. and Baker, H.G. (1983) Insects as flower visitors and pollinators. *Annual Review of Entomology* 28, 407–453.

Khan, Z.R., Ampong-Nyarko, K. *et al.* (1997) Intercropping increases parasitism of pests. *Nature* 388, 631–632.

Kfir, R. (1997) Competitive displacement of *Busseola fusca* by *Chilo partellus*. *Annals of the Entomological Society of America* 90, 619–624.

Kfir, R. (1998) Origin of the diamondback moth (Lepidoptera: Plutellidae). *Annals of the Entomological Society of America* 91, 164–167.

Kfir, R., Podoler, H. *et al.* (1976) The area of discovery and searching strategy of a primary parasite and two hyperparasites. *Ecological Entomology* 1, 287–295.

Kfir, R., Overholt, W.A. *et al.* (2002) Biology and management of economically important lepidopteran cereal stem borers in Africa. *Annual Review of Entomology* 47, 701–731.

Kidd, N.A.C. and Jervis, M.A. (1996) Population dynamics. In: Jervis, M.A. and Kidd, N.A.C. *Insect Natural Enemies: Practical Approaches to their Study and Evaluation*. London, UK: Chapman and Hall, pp. 293–374.

Kim, J-Y. (1997) Female size and fitness in the leafcutter bee *Megachile apicalis*. *Ecological Entomology* 22, 275–282.

Kindvall, O. (1999) Dispersal in a metapopulation of the bush cricket, *Metrioptera bicolor* (Orthoptera: Tettigoniidae). *Journal of Animal Ecology* 68, 172–185.

King, E.G. and Coleman, R.J. (1989) Potential for biological control of *Heliothis* species. *Annual Review of Entomology* 34, 53–75.

King, E.W. (1972) Rainfall and epidemics of the southern pine beetle. *Environmental Entomology* 1, 279–285.

King-Hele, D. (1999) *Erasmus Darwin*. London, UK: Giles de la Mare.

Kingsolver, J.G. (1987) Mosquito host choice and the epidemiology of malaria. *The American Naturalist* 130, 811–827.

Kingsolver, J.G., Hoekstra, H.E. *et al.* (2001) The strength of phenotypic selection in natural populations. *The American Naturalist* 157, 245–261.

Kinoshita, G.B., Svec, H.J. *et al.* (1979) Biology of the crucifer flea beetle, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae), in southwestern Ontario. *The Canadian Entomologist* 111, 1395–1407.

Kirk, W.D.J. (1987) How much pollen can thrips destroy? *Ecological Entomology* 12, 31–40.

Kirk, W.D.J. (1991) The size relationship between insects and their hosts. *Ecological Entomology* 16, 351–359.

Kirkpatrick, M. and Lande, R. (1989) The evolution of maternal characters. *Evolution* 43, 485–503.

Kirkpatrick, M. and Ravigne, V. (2002) Speciation by natural and sexual selection: models and experiments. *The American Naturalist* 159, S22–S35.

Kirkpatrick, T.W. (1957) *Insect Life in the Tropics*. London, UK: Longman and Green.

Kisimoto, R. (1956) Effect of crowding during the larval period on the determination of the wingform in an adult plant-hopper. *Nature* 178, 641–642.

Kisimoto, R. (1984) Insect pests of the rice plant in Asia. *Protection Ecology* 7, 83–104.

Kisimoto, R. and Sogawa, K. (1995) Migration of the brown planthopper *Nilaparvata lugens* and the white-backed planthopper *Sogatella furcifera* in East Asia: the role of weather and climate. In: Drake, V.A. and Gatehouse, A.G. (eds), *Insect Migration*. Cambridge, UK: Cambridge University Press, pp. 67– 91.

Klein, A-M., Vaissière, B.E. *et al.* (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B* 274, 303–313.

Klemperer, H.G. (1983a) The evolution of parental behaviour in Scarabaeinae (Coleoptera, Scarabaeidae): an experimental approach. *Ecological Entomology* 8, 49–59.

Klemperer, H.G. (1983b) Brood ball construction by the non-brooding Coprini *Sulcophanaeus carnifex* and *Dichotomius torulosus* (Coleoptera, Scarabaeidae). *Ecological Entomology* 8, 61–68.

Kline, M. (1972) *Mathematical Thought from Ancient to Modern Times*, vol. 1. Oxford, UK, Oxford University Press.

Klingenberg, C.P. and Spence, J.R. (1997) On the role of body size for life-history evolution. *Ecological Entomology* 22, 55–68.

Klinkhamer, P.G.L. and de Jong, T.J. (1993) Attractiveness to pollinators: a plant's dilemma. *Oikos* 66, 180–184.

Klomp, H. (1959) Infestations of forest insects and the role of parasites. Proceedings of the 15th International Congress of Zoology, London (1958), 797–800.

Klomp, H. (1966) The dynamics of a field population of the pine looper, *Bupalus piniarius* L. (Lep., Geom.) *Advances in Ecological Research* 3, 207–305.

Klug, T., Meyhöfer, R. *et al.* (2008) Native parasitoids and their potential to control the invasive leaf-miner, *Cameraria ohridella* Desch. & Dim. (Lep: Gracillariidae). *Bulletin of Entomological Research* 98, 379–387.

Klvana, I., Berteaux, D. *et al.* (2004) Porcupine feeding scars and climatic data show ecosystem effects of the solar cycle. *The American Naturalist* 164, 283–297.

Knerer, G. and Atwood, C.E. (1973) Diprionid sawflies: polymorphism and speciation. *Science* 179, 1090–1099.

Knipling, E.F. (1955) Possibilities of insect control or eradication through the use of sexually sterile males. *Journal of Economic Entomology* 48, 459–462.

Knipling, E.F. (1979) *The Basic Principles of Insect Population Suppression and Management*. Washington, DC, USA: US Department of Agriculture.

Knoll, A.H. (1986) Patterns of change in plant communities through geological time. In: Diamond,

J. and Case, T.J. (eds) *Community Ecology*. New York, New York, USA: Harper and Row, pp. 126–141.

Koch, H. and Schmid-Hempel, P. (2012) Gut microbiota instead of host genotype drive the specificity in the interaction of a natural host-parasite system. *Ecology Letters* 15, 1095–1103.

Koenig, W.D. (2002) Global patterns of environmental synchrony and the Moran effect. *Ecography* 25, 283–288.

Kogan, M. (1998) Integrated pest management: historical perspectives and contemporary developments. *Annual Review of Entomology* 43, 243–270.

Kokko, H. and López-Sepulcre, A. (2006) From individual dispersal to species ranges: perspectives for a changing world. *Science* 313, 789–791.

Kolliker-Ott, U.M., Blows, M.W. *et al.* (2003) Are wing size, wing shape and asymmetry related to field fitness of *Trichogramma* egg parasitoids? *Oikos* 100, 563–573.

Koopman, K.F. (1950) Natural selection for reproductive isolation between *Drosophila pseudoobscura* and *Drosophila persimilis*. *Evolution* 4, 135–148.

Köppen, W. (1873) Über mehrjährige Perioden der Witterung, insbesondere über die 11-jährige Periode der Temperatur. *Österreichische Gesellschaft für Meteorologie* 8, 241–248.

Kost, C. and Heil, M. (2006) Herbivore-induced plant volatiles induce an indirect defence in neighbouring plants. *Journal of Ecology* 94, 619–628.

Kowalski, R. (1977) Further elaboration of the winter moth population models. *Journal of Animal Ecology* 46, 471–482.

Koyama, J., Kakinohana, H. *et al.* (2004) Eradication of the melon fly, *Bactrocera cucurbitae*, in Japan: importance of behavior, ecology, genetics and evolution. *Annual Review of Entomology* 49, 331–349.

Krafsur, E.S. and Moon, R.D. (1997) Bionomics of the face fly, *Musca autumnalis*. *Annual Review of Entomology* 42, 503–523.

Kramer, L.D., Styer, L.M. *et al.* (2008) A global perspective on the epidemiology of West Nile Virus. *Annual Review of Entomology* 53, 61–81.

Krasnov, B.R., Poulin, R. *et al.* (2005) Host specificity and geographical range in haematophagous ectoparasites. *Oikos* 108, 449–456.

Krauss, J., Schmitt, T. *et al.* (2004) Effects of habitat fragmentation on the genetic structure of the monophagous butterfly *Polyommatus coridon* along its northern range margin. *Molecular Ecology* 13, 311–320.

Krebs, C.J. (1972) *Ecology: The Experimental Analysis of Distribution and Abundance*. New York, USA: Harper and Row.

Kremen, C., Williams, N.M. *et al.* (2002) Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences USA* 99, 16812–16816.

Kring, J.B. (1972) Flight behavior of aphids. *Annual Review of Entomology* 17, 461–492.

Kritsky, G. (1991) Darwin's Madagascan hawk moth prediction. *American Entomologist* 37, 206–210.

Kroemer, J.A. and Webb, B.A. (2004) Polydnavirus genes and genomes: emerging gene families and new insights into polydnavirus replication. *Annual Review of Entomology* 49, 431–456.

Krombein, K.V. (1967) *Trapnesting Wasps and Bees - Life Histories, Nests and Associates*. Washington, DC, USA: Smithsonian.

Kronforst, M.R., Young, L. *et al.* (2006) Multilocus analyses of admixture and introgression among hybridising *Heliconius* butterflies. *Evolution* 60, 1254–1268.

Krummel, J.R., Gardner, R.H. *et al.* (1987) Landscape patterns in a disturbed environment. *Oikos* 48, 321–324.

Kulman, H.M. (1971) Effects of insect defoliation on growth and mortality of trees. *Annual Review of Entomology* 16, 289–324.

Kumar, P.S. and Verghese, A. (2015) *Cyrtobagous salviniae* – godsend in God's Own Country. *Antenna* 39, 175–177.

Kuno, E. and Dyck, V.A. (1985) Dynamics of Philippine and Japanese populations of the brown planthopper: comparison of basic characteristics. *Chinese Journal of Entomology* 4, 1–9.

Kunte, K. (2008) Mimetic butterflies support Wallace's model of sexual dimorphism. *Proceedings of the Royal Society B* 275, 1617–1624.

Kuusijärvi, A., Hardwick, B. *et al.* (2015) A stable, genetically determined colour dimorphism in the dung beetle *Aphodius depressus*: patterns and mechanisms. *Ecological Entomology* 40, 575–584.

Kuussaari, M., Nieminen, M. *et al.* (1996) An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology* 65, 791–801.

Kvedaras, O.L., Keeping, M.G. *et al.* (2007) Larval performance of the pyralid borer *Eldana saccharina* Walker and stalk damage in sugarcane: influence of plant silicon, cultivar and feeding site. *International Journal of Pest management* 53, 183–194.

Labandeira, C.C. (1997) Insect mouthparts: ascertaining the paleobiology of insect feeding strategies. *Annual Review of Ecology and Systematics* 28, 153–193.

Labandeira, C.C. and Sepkoski, J.J. (1993) Insect diversity in the fossil record. *Science* 261, 310–315.

Lainson, R. (1983) The American leishmaniases: some observations on their ecology and epidemiology. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 77, 569–596.

Laird, M. (1981) (ed.) *Blackflies: the Future of Biological Methods in Integrated Control.* London, UK: Academic Press.Lalubin, F., Delédevant, A. *et al.* (2014) Natural malaria infection reduces starvation resistance of nutritionally stressed mosquitoes. *Journal of Animal Ecology* 83, 850–857.

Lampo, M. (1994) The importance of refuges in the interaction between *Contarinia sorghicola* and its parasitic wasp *Aprostocetus diplosidis*. *Journal of Animal Ecology* 63, 176–186.

Lamunyon, C.W. (1997) Increased fecundity, as a function of multiple mating, in an arctiid moth, *Utetheisa ornatrix*. *Ecological Entomology* 22, 69–73.

Lance, D.R., Elkinton, J.S. *et al.* (1987) Behaviour of late-instar gypsy moth larvae in high and low density populations. *Ecological Entomology* 12, 267–273.

Land, M.F. (1997) Visual acuity in insects. *Annual Review of Entomology* 42, 147–177.

Lande, R. (1976) Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30, 314–334.

Lande, R. (1982) A quantitative genetic theory of life history evolution. *Ecology* 63, 607–615.

Lande, R. and Shannon, S. (1996) The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution* 50, 434–437.

Landis, D.A., Wratten, S.D., *et al.* (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45, 175–201.

Landolt, P.J., Lenczewski, B. *et al.* (1991) Lure and toxicant system for the cabbage looper (Lepidoptera: Noctuidae). *Journal of Economic Entomology* 84, 1344–1347.

Lange, W.H. (1987) Insect pests of sugar beet. *Annual Review of Entomology* 32, 341–360.

Lange, W.H., Agosta, G.G. *et al.* (1980) Field effects of insecticides on chrysanthemum leafminer and a primary parasitoid, *Chrysocharis ainsliei* (Crawford), on artichokes in California. *Environmental Entomology* 9, 561–562.

Lanzoni, A., Accinelli, G. *et al.* (2004) Biological traits and life table of the exotic *Harmonia axyridis* compared with *Hippodamia variegata* and *Adalia bipunctata* (Col., Coccinellidae). *Journal of Applied Entomology* 128, 298–306.

Lapointe, S.L., McKenzie, C.L. *et al.* (2006) Reduced oviposition by *Diaprepes abbreviatus* (Coleoptera: Curculionidae) and growth enhancement of citrus by Surround particle film. *Journal of Economic Entomology* 99, 109–116.

Lara, A. and Villalba, R. (1993) A 3620-year temperature record from Fitzroya cupressoides tree rings in southern South America. *Science* 260, 1104–1106.

Larson, B.M.H., Kevan, P.G. *et al.* (2001) Flies and flowers: taxonomic diversity of anthophiles and pollinators. *The Canadian Entomologist* 133, 439–465.

Larsson, S. and Ekbom, B. (1995) Oviposition mistakes in herbivorous insects: confusion or a step towards a new host plant? *Oikos* 72, 155–160.

Laughlin, R. (1963) Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). VIII. Temperature and larval growth. *Bulletin of Entomological Research* 54, 745–759.

Laughlin, R. (1965) Capacity for increase: a useful population statistic. *Journal of Animal Ecology* 34, 77–91.

Laurence, B.R. (1952) The prey of some Empididae and Dolichopodidae (Dipt.). *Entomologist's Monthly Magazine* 88, 156–157.

Lawrence, W.S. (1990) The effect of group size and host species on development and survivorship of a gregarious caterpillar *Halisidota carye* (Lepidoptera: Arctiidae). *Ecological Entomology* 15, 53–62.

Laws, A.N and Joern, A. (2012) Variable effects of dipteran parasitoids and management treatment on grasshopper fecundity in a tallgrass prairie. *Bulletin of Entomological Research* 102, 123–130.

Lawton, J.H. (1982) Vacant niches and unsaturated communities: a comparison of bracken herbivores at sites on two continents. *Journal of Animal Ecology* 51, 573–595.

Lawton, J.H. (1983) Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology* 28, 23–39.

Lawton, J.H. (1986) The effect of parasitoids on phytophagous insect communities. In: Waage, J.K. and Greathead, D.J. (eds) *Insect Parasitoids*. London, UK: Academic Press, pp. 265–287.

Lawton, J. H. (1988) More time means more variation. *Nature* 334, 563.

Lawton, J.H. (1992) There are not 10 million kinds of population dynamics. *Oikos* 63, 337–338.

Lawton, J.H. (1996) Patterns in ecology. *Oikos* 75, 145–147.

Lawton, J.H. (1999) Are there general laws in ecology? *Oikos* 84, 177–192.

Lawton, J.H. and Hassell, M.P. (1981) Asymmetrical competition in insects. *Nature* 289, 793–795.

Lawton, J.H. and Schroder, D. (1977) Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. *Nature* 265, 137–140.

Lawton, J.H. and Strong, D.R. (1981) Community patterns and competition in folivorous insects. *The American Naturalist* 118, 317–338.

Lawton, J.H., MacGarvin, M. *et al.* (1987) Effects of altitude on the abundance and species richness of insect herbivores on bracken. *Journal of Animal Ecology* 56, 147–160.

Lea, A. (1969) The population ecology of brown locusts, *Locustana pardalina* (Walk.), on fixed observation areas. *Phytophylactia* 1, 93–102.

Leakey, A.D.B. (2009) Rising atmospheric carbon dioxide concentration and the future of C_4 crops for food and fuel. *Proceedings of the Royal Society B* 276, 2333–2343.

Leatemia, J.A. and Isman, M.B. (2004) Insecticidal activity of crude seed extracts of *Annonia* spp. (Annonaceae), *Lansium domesticum* and *Sandoricum koetjape* (Meliaceae) against lepidopteran larvae. *Phytoprasitica* 34, 30–37.

Leather, S.R. (1986) Insect species richness of the British Rosaceae: the importance of host range, plant architecture, age of establishment, taxonomic isolation and species-area relationships. *Journal of Animal Ecology* 55, 841–860.

Leather, S.R. (1988) Size, reproductive potential and fecundity in insects. Things aren't as simple as they seem. *Oikos* 51, 386–389.

Leather, S.R. and Awmack, C.S. (1998) The effects of qualitative changes of individuals in the population dynamics of insects. In: Dempster, J.P. and McLean, I.F.G. (eds) (1998) *Insect Populations in Theory and Practice*. Dordrecht, Germany: Kluwer Academic Publishers.

Leather, S.R., Walters, K.F.A. *et al.* (1993) *Ecology of Insects Overwintering*. Cambridge, UK: Cambridge University Press.

Lechowicz, M.J. and Jobin, L. (1983) Estimating the susceptibility of tree species to attack by the gypsy moth, *Lymantria dispar*. *Ecological Entomology* 8, 171–183.

Lecoq, M. (1995) Forecasting systems for migrant pests. 3. Locusts and grasshoppers in West Africa and Madagascar. In: Drake, V.A. and Gatehouse, A.G. (eds) (1995) *Insect Migration: Tracking Resources Through Space and Time*. Cambridge, UK: Cambridge University Press, pp. 377–395.

Lee, D.A, (1988) Factors affecting mortality of the European corn borer, *Ostrinia nubilalis* (Hübner), in Alberta. *The Canadian Entomologist* 120, 841–853.

Lee, I.-M., Davis, R.E. *et al.* (2000) Phytoplasma: phytopathogenic mollicutes. *Annual Review of Microbiology* 54, 221–255.

Lee, R. (1978) *Forest Microclimatology*. New York, New York, USA: Columbia University Press.

Lee, R.E. (1991) Principles of insect low temperature tolerance. In: Lee, R.E. and Denlinger, D.L. (eds) *Insects at Low Temperature*. New York, New York, USA: Chapman and Hall, pp. 17–46.

Lee, R.E., Chen, C.-P. *et al.* (1987) A rapid cold-hardening response in insects. *Science* 238, 1415–1417.

Lee, R.E., Costanzo, J.P. *et al.* (1994) Ice-nucleating active bacteria reduce the cold-hardiness of the freeze-intolerant Colorado potato beetle (Coleoptera: Chrysomelidae). *Journal of Economic Entomology* 87, 377–381.

Lee, R.E., Litzgus, J.D. *et al.* (1999) Evaluation of ice-nucleating micro-organisms for reducing the supercooling capacity and cold-hardiness of *Cacopsylla pyricola* (Hemiptera: Psyllidae). *The Canadian Entomologist* 131, 715–723.

Lees, A.D. (1966) The control of polymorphism in aphids. *Advances in Insect Physiology* 3, 207–277.

Leff, B., Ramankutty, N. *et al.* (2004) Geographic distribution of major crops across the world. *Global Biochemical Cycles* 18, 1–27.

Leggett, H.C., Jones, E.O. *et al.* (2011) Population genetic structure of the winter moth, *Operophtera* *brumata* L., in the Orkney Isles suggests long-distance dispersal. *Ecological Entomology* 36, 318–325.

Lehane, M.J. (1991) *Biology of Blood-Sucking Insects*. London, UK: HarperCollins.

Lehane, M.J. and Hargrove, J. (1988) Field experiments on a new method of determining age in tsetse flies (Diptera: Glossinidae). *Ecological Entomology* 13, 319–322.

Lei, G-C. and Hanski, I. (1997) Metapopulation structure of *Cotesia melitaearum*, a specialist parasitoid of the butterfly *Melitaea cinxia*. *Oikos* 78, 91–100.

Leigh, E.G. Jr (1970) Sex ratio and differential mortality between the sexes. *The American Naturalist* 104, 205–210.

Leigh, E.G. (1975) Structure and climate in tropical rain forest. *Annual Review of Ecology and Systematics* 6, 67–86.

Leonard, D.E. (1970) Intrinsic factors causing qualitative changes in populations of the gypsy moth. *Canadian Entomologist* 102, 239–249.

LeRoux, E.J., Paradis, R.O. *et al.* (1963) Major mortality factors in the population dynamics of the eye-spotted bud-moth, the pistol casebearer, the fruit-tree leaf roller, and the European corn borer in Quebec. *Memoirs of the Entomological Society of Canada* 32, 67–82.

Le Ru, B.P., Ong'amo, G.O. *et al.* (2006) Diversity of lepidopteran stem borers on mono-cotyledonous plants in eastern Africa and the islands of Madagascar and Zanzibar revisited. *Bulletin of Entomological Research* 96, 555–563.

Leskey, T.C. and Wright, S.E. (2004) Monitoring plum curculio, *Conotrachelus nenuphar* (Coleoptera: Curculionidae), populations in apple and peach orchards in the Mid-Atlantic [States]. *Journal of Economic Entomology* 97, 79–88.

Leslie, P.H. and Ranson, R.M (1940) The mortality, fertility and rate of natural increase of the vole (*Microtus agrestis*) as observed in the laboratory. *Journal of Animal Ecology* 9, 27–52.

Lessells, C.M. (1985) Parasitoid foraging: should parasitism be density dependent? *Journal of Animal Ecology* 54, 27–41.

Levi, H.W. and Levi, L.R. (1968) *Spiders and their Kin*. New York, New York, USA: Golden Press.

Levin, S.A. (1976) Population dynamics in heterogeneous environments. *Annual Review of Ecology and Systematics* 7, 287–310.

Levin, S.A. (1980) Mathematics, ecology, and ornithology. *Auk* 97, 422–425.

Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology* 73, 1943–1967.

Levine, S. (1980) Several measures of trophic structure applicable to complex food webs. *Journal of Theoretical Biology* 83, 195–207.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15, 237–240.

Levins, R. (1970) Extinction. In: Gerstenhaben, M. (ed.) *Some Mathematical Problems in Biology*. Providence, Rhode Island, USA: Mathematical Society, pp. 77–107.

Levins, R. and Culver, D. (1971) Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences USA* 68, 1246–1248.

Levins, R. and MacArthur, R.H. (1969) A hypothesis to explain the incidence of monophagy. *Ecology* 30, 910–911.

Lewin, R. (1993) *Complexity: Life on the Edge of Chaos*. London, UK: Phoenix.

Lewis, A.C. (1984) Plant quality and grasshopper feeding: effects of sunflower condition on preference and performance in *Melanoplus differentialis*. *Ecology* 65, 836–843.

Lewis, T. (1997) *Thrips as Crop Pests*. Wallingford, UK: CAB International.

Lewis, T. and Macaulay, E.D.M. (1976) Design and elevation of sex-attractant traps for pea moth, *Cydia nigricana* (Steph.) and the effect of plume shape on catches. *Ecological Entomology* 1, 175–187.

Lewis, T. and Taylor, L.R. (1967) *Introduction to Experimental Ecology*. London, UK: Academic Press.

Lewontin, R.C. (1965) Selection for colonising ability. In: Baker, H.G. and Stebbins, G.L. (eds) *The Genetics of Colonising Species*. New York, New York, USA: Academic Press, pp. 77–91.

Lewontin, R.C. (1970) The units of selection. *Annual Review of Ecology and Systematics* 1, 1–18.

Li, J. and Newbigin, E. (2002) Self-incompatibility in flowering plants: the ribonuclease-based systems. *Annual Plant Reviews* 6, 257–278.

Li, Z.M., Liu, S.S. *et al.* (2007) Temperature-related fitness costs of resistance to spinosad in the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Bulletin of Entomological Research* 97, 627–635.

Libersat, F., Delago, A. *et al.* (2009) Manipulation of host behavior by parasitic insects and insect parasites. *Annual Review of Entomology* 54, 189–207.

Lidicker, W.Z. (1962) Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. *The American Naturalist* 96, 29–33.

Liebhold, A.M., Koenig, W.D. *et al.* (2004) Spatial synchrony in population dynamics. Annual *Review of Ecology, Evolution and Systematics* 35, 467–490.

Liebhold, A.M. and Tobin, P.C. (2008) Population ecology of insect invasions and their management. *Annual Review of Entomology* 53, 387–408.

Liepert, C. and Dettner, K. (1993) Recognition of aphid parasitoids by honeydew-collecting ants: the role of cuticular lipids in chemical mimicry systems. *Journal of Chemical Ecology* 19, 2143–2153.

Liepert, C. and Dettner, K. (1996) Role of cuticular hydrocarbons of aphid parasitoids in their relationship to aphid-attending ants. *Journal of Chemical Ecology* 22, 695–707.

Lieutier, F., Day, K.R. *et al.* (eds) (2004) *Bark and Wood Boring Insects in Living Trees in Europe: A Synthesis*. New York, New York, USA: Springer.

Liew, C. and Curtis, C.F. (2004) Horizontal and vertical dispersal of dengue vector mosquitoes, *Aedes aegypti* and *Aedes albopictus*, in Singapore. *Medical and Veterinary Entomology* 18, 351–360.

Lill, J.T. and Marquis, R.J. (2003) Ecosystem engineering by caterpillars increases insect herbivore diversity on white oaks. *Ecology* 84, 682–690.

Lim, K.P., Yule, W.N. *et al.* (1980) A note on *Pelecinus polyturator* (Hymenoptera: Pelecinidae), a parasite of *Phyllophaga anxia* (Coleoptera: Scarabaeidae). *The Canadian Entomologist* 112, 219.

Lima, S.L. (1998) Non-lethal effects in the ecology of predator-prey interactions. *Bioscience* 48, 25–34.

Lincoln, C., Dean, G. *et al.* (1971) Resistance of frego-type cotton to boll weevil and bollworm. *Journal of Economic Entomology* 64, 1326–1327.

Lincoln, R.J., Boxshall, G.A. *et al.* (1982) *A Dictionary of Ecology, Evolution and Systematics*. Cambridge, UK: Cambridge University Press.

Lindblad, M. and Areno, P. (2002) Temporal and spatial population dynamics of *Psammotettix alienus*, a vector of wheat dwarf virus. *International Journal of Pest Management* 48, 233–238.

Lindquist, D.A., Abusowa, M. *et al.* (1992) The New World screwworm fly in Libya. *Medical and Veterinary Entomology* 6, 2–8.

Linit, M.J. and Stephen, F.M. (1983) Parasite and predator component of within-tree southern pine beetle (Coleoptera: Scolytidae) mortality. *The Canadian Entomologist* 115, 679–688.

Linley, J.R., Evans, H.T. *et al.* (1970) A quantitative study of autogeny in a naturally occurring population of *Culicoides furens* (Poey) (Diptera: Ceratopogonidae). *Journal of Animal Ecology* 39, 169–183.

Linsley, E.G. (1959) Ecology of Cerambycidae. *Annual Review of Entomology* 4, 99–138.

Linsley, E.G. (1962) Sleeping aggregations of aculeate Hymenoptera-2. *Annals of the Entomological Society of America* 55, 148–164.

Litsios, S. (1996) *The Tomorrow of Malaria*. Wellington, New Zealand: Pacific Press.

Liu, H., Ellington, C.P. *et al.* (1998) A computational, fluid dynamic study of hawkmoth hovering. *The Journal of Experimental Biology* 201, 461–477.

Lloyd, M. (1967) Mean crowding. *Journal of Animal Ecology* 36, 1–30.

Lloyd, M. (1984) Periodical cicadas. *Antenna* 8, 79–91.

Lloyd, M. and Ghelardi, R.J. (1964) A table for calculating the "equitability" component of species diversity. *Journal of Animal Ecology* 33, 217–225.

Loan, C. (1963) The bionomics of *Sitona scissifrons* (Coleoptera: Curculionidae) and its parasite *Microctonus sitonae* (Hymenoptera: Braconidae). *Annals of the Entomological Society of America* 56, 600–612.

Lockwood, J.A. (1993) Environmental issues involved in biological control of rangeland grasshoppers (Orthoptera: Acrididae) with exotic agents. *Environmental Entomology* 22, 503–518.

Lomer, C.J., Bateman, R.P. *et al.* (2001) Biological control of locusts and grasshoppers. *Annual Review of Entomology* 46, 667–702.

Łomniki, A. (1978) Individual differences between animals and the natural regulation of their numbers. *Journal of Animal Ecology* 47, 461–675.

Łomniki, A. (1980) Regulation of population density due to individual differences and patchy environment. *Oikos* 35, 185–193.

Łomniki, A. (1988) *Population Ecology of Individuals*. Princeton, New Jersey, USA: Princeton University Press.

Long, S.J., Williams, D.W. *et al.* (2009) *Sirex* species (Hymenoptera: Siricidae) and their parasitoids in *Pinus sylvestris* in eastern North America. *The Canadian Entomologist* 141, 153–157.

Long, W.H. and Hensley, S.D. (1972) Insect pests of sugar cane. *Annual Review of Entomology* 17, 149–176.

Lorenz, K. (1965) *Evolution and Modification of Behaviour*. Chicago, Illinois, USA: Chicago University Press.

Losey, J.E., Ives, A.R. *et al.* (1997) A polymorphism maintained by opposite patterns of parasitism and predation. *Nature* 388, 269–272.

Lotka, A.J. (1920) Analytical note on certain rhythmic reactions in organic systems. *Proceedings of the National Academy of Sciences USA* 6, 410–415.

Lotka, A.J. (1925) *Elements of Physical Biology*. Baltimore, Maryland, USA: Williams and Wilkins.

Louda, S.M., Pemberton, R.W. *et al.* (2003) Nontarget effects – the Achilles' heel of biological control? *Annual Review of Entomology* 48, 365–396.

Lounibos, L.P., Martin, E.A. *et al.* (1998) Daylength and temperature control of predation, body size, and rate of increase in *Toxorhynchites rutilus* (Diptera: Culicidae). *Annals of the Entomological Society of America* 91, 308–314.

Lövei, G.L. and Arpaia, S. (2005) The impact of transgenic plants on natural enemies: a critical review of laboratory studies. *Entomologia Experimentalis et Applicata* 114, 1–14.

Lövei, G.L. and Sunderland, K.D. (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology* 41, 231–256.

Lovell, J.H. (1914) The origin of oligotropism (Hymen.). *Entomological News* 25, 314–321.

Lovett, R.A. (2002) Rain might be a leading carbon sink factor. *Science* 296, 1787.

Loxdale, H.D. (2007) Big issues in population biology: lessons from a greenfly. *Antenna* 31, 194–202.

Lubbock, J. (1874) *The Origin and Metamorphosis of Insects*. London, UK: MacMillan.

Lucarotti, C.J., Eveleigh, E.S. *et al.* (2004) Prevalence of baculoviruses in spruce budworm (Lepidoptera: Tortricidae) populations in New Brunswick. *The Canadian Entomologist* 136, 255–264.

Luck, R.F. and Podoler, H. (1985) Competitive exclusion of *Aphytis lingnanensis* by *A. melinus*: potential role of host size. *Ecology* 66, 904–913.

Luck, R.F., Shepard, B.M. *et al.* (1988) Experimental methods for evaluating arthropod natural enemies. *Annual Review of Entomology* 33, 367–391.

Ludy, C. and Lang, A. (2006) Bt maize pollen impact on the garden spider, *Araneus diadematus*. *Entomologia Experimentalis et Applicata* 118, 145–156.

Luff, M.L. (1976) The biology of *Microctonus caudatus* (Thomson), a braconid parasite of the ground beetle *Harpalus rufipes* (Degeer). *Ecological Entomology* 1, 111–116.

Luff, M.L. (1978) Diel activity patterns of some field Carabidae. *Ecological Entomology* 3, 53–62.

Luff, M.L. (1982) Population dynamics of Carabidae. *Annals of Applied Biology* 101, 164–170.

Luff, M.L. (2007) *The Carabidae (ground beetles) of Britain,* 2nd edn. *Handbooks for the Identification of British Insects* 4(2), i–iv, 1–247. London, UK: Royal Entomological Society.

Lundberg, P. and Astrom, M. (1990) Low nutritive quality as a defense against optimally foraging herbivores. *The American Naturalist* 135, 547–562.

Luttrell, R.G. (1994) Cotton pest management: Part 2. A US perspective. *Annual Review of Entomology* 39, 527–542.

Luttrell, R.G., Fitt, G.P. *et al.* (1994) Cotton pest management: Part 1. A worldwide perspective. *Annual Review of Entomology* 39, 517–526.

Lynch, L., Bowers, R.G. *et al.* (1998) A dynamic refuge model and population regulation by insect parasitoids. *Journal of Animal Ecology* 67, 270–279.

Lynch, L.D., Ives, A.R. *et al.* (2002) The risks of biocontrol: transient impacts and minimum non-target densities. *Ecological Applications* 12, 1872–1882.

Lyttle, T.W. (1977) Experimental population genetics of meiotic drive systems. 1. Pseudo-Y chromosomal drive as a means of eliminating caged populations of *Drosophila melanogaster*. *Genetics* 86, 413–445.

Lyytinen, A., Boman, S. *et al*. (2009) Cold tolerance during larval development: effects on the thermal distribution limits of *Leptinotarsa decemlineata*. *Entomologia Experimentalis et Applicata* 133, 92–99.

Ma, M., Burkholder, W.E. *et al*. (1978) Supra-anal organ: a defensive mechanism of the furniture carpet beetle, *Anthrenus flavipes* (Coleoptera: Dermestidae). *Annals of the Entomological Society of America* 71, 718–723.

Ma, S.C. (1958) The population dynamics of the oriental migratory locust (*Locusta migratoria manilensis* Meyen). *Acta Entomologica Sinica* 8, 1–40.

Maad, J. and Nilsson, L.A. (2004) On the mechanism of floral shifts in speciation: gained pollination efficiency from tongue- to eye-attachment of pollinia in *Platanthera* (Orchidaceae). *Biological Journal of the Linnean Society* 83, 481–495.

Macagno, A.L.M., Boano, G. *et al*. (2008) Movement and demographics of *Libellula fulva* (Odonata: Libellulidae). *Environmental Entomology* 37, 1145–1153.

MacArthur, R.H. (1955) Fluctuations of animal populations, and a measure of community stability. *Ecology* 36, 533–536.

MacArthur, R.H. (1960) On the relative abundance of species. *The American Naturalist* 94, 25–36.

MacArthur, R.H. (1965) Patterns of species diversity. *Biological Reviews* 40, 510–533.

MacArthur, R.H. (1972) *Geographical Ecology: Patterns in the Distribution of Species*. New York, New York, USA: Harper and Row.

MacArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton, New Jersey, USA: Princeton University Press.

MacDonald, C. and Loxdale, H.D. (2004) Molecular markers to study population structure in beneficial insects (predators and parasitoids). *International Journal of Pest Management* 50, 215–224.

Macdonald, D. (ed.) (1984) *The Encyclopaedia of Mammals*. London, UK: Allen and Unwin.

Macdonald, D.W. and Smith, H. (1990) New perspectives on agro-ecology: between theory and practice in the agricultural ecosystem. In: Firbank, L.G., Carter, N. *et al*. (eds) *The Ecology of Temperate Cereal Fields*. London, UK: Blackwell, pp. 413–448.

Macdonald, G. (1957) *The Epidemiology and Control of Malaria*. London, UK: Oxford University Press.

MacFadyen, A. (1957) *Animal Ecology: Aims and Methods*. London, UK: Pitman.

MacHardy, W.E. (2000) Current status of IPM in apple orchards. *Crop Protection* 19, 801–806.

MacLellan, C.R. (1977) Trends of codling moth (Lepidoptera: Olethreutidae) populations over 12 years on two cultivars in an insecticide free orchard. *The Canadian Entomologist* 109, 1555–1562.

MacLeod, A., Wratten, S.D. *et al*. (2004) "Beetle banks" as refuges for beneficial arthropods in farmland: long-term changes in predator communities and habitat. *Agricultural and Forest Entomology* 6, 147–154.

MacPhee, A., Newton, A. *et al*. (1988) Population studies on the winter moth *Operophtera brumata* (L.) (Lepidoptera: Geometridae) in apple orchards in Nova Scotia. *The Canadian Entomologist* 120, 73–83.

Maelzer, D.A. (1965) A discussion of components of environment in ecology. *Journal of Theoretical Biology* 8, 141–162.

Maeno, K. and Tanaka, S. (2008) Phase-specific developmental and reproductive strategies in the desert locust. *Bulletin of Entomological Research* 98, 527–534.

Magurran, A.E. (2004) *Measuring Biological Diversity*. Oxford, UK: Blackwell.

Mair, L., Thomas, C.D. *et al*. (2015) Quantifying the activity levels and behavioural responses of butterfly species to habitat boundaries. *Ecological Entomology* 40, 823–828.

Majerus, M.E.N. (1994) *Ladybirds*. London, UK: HarperCollins.

Majerus, M.E.N. and Hurst, G.D.D. (1997) Ladybirds as a model system for the study of male-killing symbionts. *Entomophaga* 42, 13–20.

Malausa, T., Pélissié, B. *et al*. (2008) Differences in oviposition behaviour of two sympatric species of the genus *Ostrinia*. *Bulletin of Entomological Research* 98, 193–201.

Mallet, J. (1995) A species definition for the modern synthesis. *Trends in Ecology and Evolution* 10, 294–299.

Mallet, J. (2004) Perspectives: Poulton, Wallace and Jordan: how discoveries in *Papilio* butterflies led to a new species concept. *Systematics and Biodiversity* 1, 441–452.

Mallet, J. (2005) Hybridisation as an invasion of the genome. *Trends in Ecology and Evolution* 20, 229–237.

Mallet, J. (2009) Alfred Russel Wallace and the Darwinian species concept: his paper on the swallowtail butterflies (Papilionidae) of 1865. *Gayana* 73, (Suppl.) 42–54.

Mallet, J. and Joron, M. (1999) Evolution of diversity in warning color and mimicry: polymorphism, shifting balance, and speciation. *Annual Review of Ecology and Systematics* 30, 201–233.

Mallinger, R.E. and Gratton, C. (2015) Species richness of wild bees, but not the use of managed honey bees, increases fruit set of a pollinator-dependent crop. *Journal of Applied Ecology* 52, 325–230.

Malthus, T.R. (1798) *An Essay of the Principle of Population as it Affects the Future Improvement of Society*. London, UK: J. Johnson.

Malyshev, S.I. (1968) In Richards, O.W. and Uvarov, B (eds) *Genesis of the Hymenoptera and the Phases of their Evolution*, English edn. London, UK: Methuen.

Mampe, C.D. and Neunzig, H.H. (1967) The biology, parasitism and population sampling of the plum curculio on blueberry in North Carolina. *Journal of Economic Entomology* 60, 807–812.

Mandelbrot, B.B. (1977) *Fractals; Form, Chance and Dimension*. San Francisco, California, USA: Freeman.

Mankin, R.W. and Benshemesh, J. (2006) Geophone detection of subterranean termite and ant activity. *Journal of Economic Entomology* 99, 244–250.

Manley, G.V. (1971) A seed-caching carabid (Coleoptera). *Annals of the Entomological Society of America* 64, 1474–1475.

Manly, B.F.J. (1990*) Stage-structured Populations, Sampling, Analysis and Simulation*. London, UK: Chapman and Hall.

Mann, B.P., Wratten, S.D. *et al.* (1991) The economics of reduced-rate insecticide applications to control aphids on winter wheat. *Annals of Applied Biology* 119, 451–464.

Manson, P. (1878) On the development of *Filaria sanguinis hominis* and on the mosquito considered as a nurse. *Journal of the Linnean Society (Zoology)* 14, 304–311.

Mansour, F., Rosen, D. *et al.* (1981) Disturbing effect of a spider on larval aggregations of *Spodoptera littoralis*. *Entomologia Experimentalis et Applicata* 29, 234–237.

Marden, J.H. (1987) Maximum lift production during take off in flying animals. *The Journal of Experimental Biology* 130, 235–258.

Marden, J. H. (2000) Variability in the size, composition and function of insect flight muscles. *Annual Review of Physiology* 62, 157–178.

Marden, J.H. and Chai, P. (1991) Aerial predation and butterfly design: how palatability, mimicry, and the need for evasive flight constrain mass allocation. *The American Naturalist* 138, 15–36.

Marden, J.H., Fitzhugh, G.H. *et al.* (1998) From molecules to mating success: integrative biology of muscle maturation in a dragonfly. *American Zoologist* 38, 528–544.

Margalef, R. (1963) On certain underlying principles in ecology. *The American Naturalist* 97, 357–374.

Margalef, R. (1968) *Perspectives in Ecological Theory*. Chicago, Illinois, USA: The University of Chicago Press.

Margolis, H. (1993) *Paradigms and Barriers: How Habits of Mind Govern Scientific Beliefs*. Chicago, Illinois, UK: The University of Chicago Press.

Margules, C.R. and Pressey, R.L. (2000) Systematic conservation planning. *Nature* 405, 243–253.

Marquis, R.J. and Lill, J.T. (2007) Effects of arthropods as physical ecosystem engineers on plant-based trophic interaction webs. In: Ohgushi, T., Craig, T.P. *et al.* (eds), *Indirect Interaction Webs: Nontrophic Linkages Through Induced Plant Traits*. Cambridge, UK: Cambridge University Press, pp. 246–274.

Marquis, R.J. and Whelan, C.J. (1994) Insectivorous birds increase growth of white oaks through consumption of leaf chewing insects. *Ecology* 75, 2007–2014.

Marrelli, M.T., Li, C. *et al.* (2007) Transgenic malaria-resistant mosquitoes have a fitness advantage when feeding on *Plasmodium*-infected blood. *Proceedings of the National Academy of Sciences USA* 104, 5580–5583.

Marsteller, S., Adams, D. *et al.* (2009) Six cryptic species on a single species of host plant: morphometric evidence for possible reproductive character displacement. *Ecological Entomology* 34, 66–73.

Martin, J.L. (1956) The bionomics of the aspen blotch, *Lithocolletis salicifoliella* Cham. (Lepidoptera:

Gracillariidae). *The Canadian Entomologist* 88, 155–168.

Martin, M.M. (1987) *Invertebrate Microbial Interactions*. New York, New York, USA: Cornell University Press.

Martin, M.M. (1991) The evolution of cellulose digestion in insects. *Philosophical Transactions of the Royal Society B* 333, 281–288.

Martin, S.J. (2012) The butterfly, owl or lizard? *Antenna* 36, 219–220.

Martinat, P.J. and Allen, D.C. (1987) Relationship between outbreaks of saddled prominent, *Heterocampa guttivitta* (Lepidoptera: Notodontidae), and drought. *Environmental Entomology* 16, 246–249.

Martini, X., Haccou, P. *et al*. (2009) Evolution of cannibalism and female's response to oviposition-deterring pheromone in aphidophagous predators. *Journal of Animal Ecology* 78, 964–972.

Masaki, M., Ohmura, K. *et al*. (1984) Host range studies of the black vine weevil, *Otiorhynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae). *Applied Entomology and Zoology* 19, 95–106.

Mason, P.G., Miall, P. *et al*. (2011) Parasitoid communities associated with an invasive canola pest, *Ceutorhynchus obstrictus* (Coleoptera: Curculionidae), in Ontario and Quebec, Canada. *The Canadian Entomologist* 143, 524–537.

Mason, R.R. (1974) Population change in an outbreak of the Douglas-fir tussock moth, *Orgyia pseudostugata* (Lepidoptera: Lymantriidae), in central Arizona. *The Canadian Entomologist* 106, 1171–1174.

Mason, R.R. (1976) Life tables for a declining population of the Douglas-fir tussock moth in Northeastern Oregon. *Annals of the Entomological Society of America* 69, 948–958.

Mason, R.R. (1978) Synchronous patterns in an outbreak of the Douglas-fir tussock moth. *Environmental Entomology* 7, 672–675.

Massey, F.P., Ennos, A.R. *et al*. (2006) Silica in grasses as a defence against insect herbivores: contrasting effects on folivores and a phloem feeder. *Journal of Animal Ecology* 75, 595–603.

Masters, G.J., Brown, V.K. *et al*. (1993) Plant mediated interactions between above- and belowground insect herbivores. *Oikos* 66, 148–151.

Masters, G.J., Jones, T.H. *et al*. (2001) Host-plant mediated effects of root herbivory on insect seed predators and their parasitoids. *Oecologia* 127, 246–250.

Mather, K. (1955) Polymorphism as an outcome of disruptive selection. *Evolution* 9, 52–61.

Matson, P.A., Parton, W.J. *et al*. (1997) Agricultural intensification and ecosystem properties. *Science* 277, 504–509.

Matsumoto, Y., Matsumura, M. *et al*. (2013) Mitochondrial *cox* sequences of *Nilaparvata lugens* and *Sogatella furcifera* (Hemiptera: Delphacidae): low specificity among Asian plant hopper populations. *Bulletin of Entomological Research* 103, 382–392.

Matsuura, M. and Yamane, S. (1984) *Biology of the Vespine Wasps*. Berlin, Germany: Springer.

Matteson, P.C. (2000) Insect pest management in tropical Asian irrigated rice. *Annual Review of Entomology* 45, 549–574.

Matthews, G.A. (1989) *Cotton Insect Pests and their Management*. Harlow, UK: Longman.

Matthews, G.A. (1994) The effects of insect attack on the yield of cotton. In: Matthews, G.A. and Tunstall, J.P. (eds) *Insect Pests of Cotton*. Wallingford, UK: CAB International, pp. 427–430.

Matthews, G.A. (2000) *Pesticide Application Methods*, 3rd edn. Oxford, UK: Blackwell Science.

Matthews, R.W. (1974) Biology of Braconidae. *Annual Review of Entomology* 19, 15–32.

Matthews, R.W., Gonzales, J.M. *et al*. (2009) Biology of the parasitoid *Melittobia* (Hymenoptera: Eulophidae). *Annual Review of Entomology* 54, 251–266.

Matthews, T.J. and Whittaker, R.J. (2015) On the species abundance distribution in applied ecology and biodiversity management. *Journal of Applied Ecology* 52, 443–454.

Mattson, W.J. (1980a) Cone resources and the ecology of the red pine cone beetle, Conophthorus resinosae (Coleoptera: Scolytidae). *Annals of the Entomological Society of America* 73, 390–396.

Mattson, W.J. (1980b) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11, 119–161.

Mattson, W.J. and Addy, N.D. (1975) Phytophagous insects as regulators of forest primary production. *Science* 190, 515–522.

Maw, M.G. (1965) Effects of air ions on duration and rate of sustained flight of the blow fly, *Phaenicia sericata* Meigen. *The Canadian Entomologist* 97, 552–556.

May, M.L. (1979) Insect thermoregulation. *Annual Review of Entomology* 24, 313–349.

May, M.L. (1991) Dragonfly flight: power requirements at high speed and acceleration. *The Journal of Experimental Biology* 158, 325–342.

May, R.M. (1973) *Stability and Complexity in Model Ecosystems*. Princeton, New Jersey, USA: Princeton University Press.

May, R.M. (1975) Estimating *r*: a pedagogical note. *The American Naturalist* 110, 496–499.

May, R.M. (1978) Host-parasitoid systems in patchy environments: a phenomenological model. *Journal of Animal Ecology* 47, 833–843.

May, R.M. and Southwood, T.R.E. (1990) Introduction. In: Shorrocks, B. and Swingland, I.R. (eds), *Living in Patchy Environments*. Oxford, UK: Oxford Science, pp. 1–22.

May, R.M. and Stumpf, M.P.H. (2000) Species-area relations in tropical forests. *Science* 290, 2084–2086.

Maynard Smith, J. (1964) Group selection and kin selection. *Nature* 201, 1145–1147.

Maynard Smith, J. (1966) Sympatric speciation. *The American Naturalist* 100, 637–650.

Maynard Smith, J. (1976) Group selection. *Quarterly Review of Biology* 51, 277–283.

Maynard Smith, J. (1978) *The Evolution of Sex*. Cambridge, UK: Cambridge University Press.

Maynard Smith, J. (1983a) The causes of extinction. *Philosophical Transactions of the Royal Society B* 325, 241–252.

Maynard Smith, J. (1983b) Models of evolution. *Proceedings of the Royal Society of London B* 219, 315–325.

Maynard Smith, J. (1989) *Evolutionary Genetics*. Oxford, UK: Oxford University Press.

Maynard Smith, J., Burian, R. *et al.* (1985) Developmental constraints and evolution. *The Quarterly Review of Biology* 60, 265–287.

Maynard Smith, J. and Szathmáry, E. (1995) *The Major Transitions in Evolution*. Oxford, UK: W.H. Freeman/Spektrum.

Mayr, E. (1942) *Systematics and the Origin of Species*. New York, New York, USA: Columbia University Press.

Mayr, E. (1963) Animal Species and Evolution. Cambridge, Massachusetts, USA: Harvard University Press.

Mayr, E. (1982) *The Growth of Biological Thought*. Cambridge, Massachusetts, USA: Harvard University Press.

Maxwell, F.G. and Jennings, P.R. (eds) (1980) *Breeding Plants Resistant to Insects*. New York, New York, USA: Wiley.

McArdle, B.H. and Gaston, K. (1995) The temporal variability of densities: back to basics. *Oikos* 74, 165–171.

McClure, M.S. (1975) Key to the eight species of coexisting *Erythroneura* leafhoppers (Homoptera: Cicadellidae) on American sycamore. *Annals of the Entomological Society of America* 68, 1039–1043.

McClure, M.S. (1991) Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. *Environmental Entomology* 20, 258–264.

McDonald, G. (1995) Insect migration in an arid continent. I. The common armyworm *Mythimna convecta* in eastern Australia. In Drake, V.A. and Gatehouse, A.G. (eds) *Insect Migration: Tracking Resources Through Space and Time*. Cambridge, UK: Cambridge University Press.

McDonogh, R.S. (1939) The habitat distribution and dispersal of the psychid moth *Luffia ferchaultella* in England and Wales. *Journal of Animal Ecology* 8, 10–28.

McIntosh, R.P. (1995) The individualistic concept. *Biological Reviews* 70, 317–357.

McKinlay, R.G. (1992) *Vegetable Crop Pests*. London, UK: Macmillan.

McKinney, M.L. (2008) Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems* 11, 161–176.

McLachlan, A. and Neems, R. (1989) An alternative mating system in small male insects. *Ecological Entomology* 14, 85–91.

McLain, D.K. (1991) The *r-K* continuum and the relative effectiveness of sexual selection. *Oikos* 60, 263–265.

McLain, D.K. and Shure, D.J. (1987) Pseudocompetition: Interspecific Displacement of Insect Species through Misdirected Courtship. *Oikos* 49, 291–296.

McNeill, S. (1973) The dynamics of a population of *Leptopterna dolabrata* (Heteroptera: Miridae) in relation to food resources. *Journal of Animal Ecology* 42, 495–507.

McNeill, W.H. (1976) *Plagues and People*. New York, New York, USA: Anchor Press/Doubleday.

McShea, D.W. (1998) Possible largest-scale trends in organismal evolution: eight "live hypotheses". *Annual Review of Ecology and Systematics* 29, 293–318.

Medawar, P. (1967) *The Art of the Soluble*. London, UK: Methuen.

Meehl, G.A. and Tebaldi, J.H. (2004) More intense, more frequent and longer lasting heat waves in the 21st century. *Science* 305, 994–997.

Megnin, P. (1894) *La Faune des Cadavres. Application de l'Entomologie a la Medicine Legale*. Paris, France: Masson et Gautier-Villars.

Melander, A.L. (1914) Can insects become resistant to sprays? *Journal of Economic Entomology* 7, 167–172.

Mellanby, K. (1939) Low temperature and insect activity. *Proceedings of the Royal Society B* 127, 473–487.

Mellor, P., Boorman, J.P.T. *et al*. (2000) Culicoides biting midges. *Annual Review of Entomology* 45, 307–340.

Memmott, J., Craze, P.G. *et al*. (2005) The effect of propagule size on the invasion of an alien insect. *Journal of Animal Ecology* 74, 50–62.

Mendeleev, D. (1869) Ueber die Beziehungen der Eigenschaften zu den Atomgewichten der Elemente. *Zeitschrift für Chemie* 12, 405–406.

Menéndez, R., Gonzáles-Megías, A. *et al.* (2008) Escape from natural enemies during climate-driven range expansion: a case study. *Ecological Entomology* 33, 413–421.

Mentis, M.T. (1988) Hypothetico-deductive and inductive approaches in ecology. *Functional Ecology* 2, 5–14.

Mercer, D.R. and Castillo-Pizango, M.J. (2005) Changes in relative species compositions of biting midges (Diptera: Ceratopogonidae) and an outbreak of Oropouche virus in Iquitos, Peru. *Journal of Medical Entomology* 42, 554–558.

Merilaita, S. (2003) Visual background complexity facilitates the evolution of camouflage. *Evolution* 57, 1248–1254.

Messenger, P.S. (1964a) The use of life tables in a bioclimatic study of an experimental aphid-braconid wasp host parasite system. *Ecology* 45, 119–131.

Messenger, P.S. (1964b) The influence of rhythmically fluctuating temperatures on the development and reproduction of the spotted alfalfa aphid, *Therioaphis maculata*. *Journal of Economic Entomology* 57, 71–76.

Metcalf, R.L. and Metcalf, R.A. (1993) *Destructive and Useful Insects: Their Habits and Control*, 5th edn. New York, New York, USA: McGraw-Hill.

Metcalfe, J.R. (1968) Studies on the biology of the sugar-cane pest *Saccharosydne saccharivora* (Westw.) (Hom.: Delphacidae). *Bulletin of Entomological Research* 59, 393–408.

Metcalfe, J.R. (1971) Observations on the ecology of *Saccharosydne saccharivora* (Westw.) (Hom.: Delphacidae) in Jamaican sugarcane fields. *Bulletin of Entomological Research* 60, 565–597.

Mettler, L.E., Gregg, T.G. *et al.* (1988) *Population Genetics and Evolution*, 2nd edn. Upper Saddle River, New Jersey, USA: Prentice-Hall.

Michaud, J.P. (2012) Coccinellids in biological control. In: Hodek, I., van Emden, H.F. *et al.* (eds) *Ecology and Behaviour of the Ladybird Beetles*. Oxford, UK: Blackwell, pp. 488–519.

Michelbacher, A.E. and Bacon, O.G. (1952) Walnut insect and spider-mite control in Northern California. *Journal of Economic Entomology*, 45, 1020–1027.

Michener, C.D. (1974) *The Social Behavior of Bees*. Cambridge, Massachusetts, USA: Harvard University Press.

Michiels, N.K. and Dhondt, A.A. (1991) Characteristics of movements in sexually mature dragonflies. *Ecological Entomology* 16, 449–459.

Miles, H.V. (1923) Observations on the bionomics of the apple blossom weevil, *Anthonomus pomorum* Linn. *Annals of Applied Biology* 10, 348–369.

Miles, P.W. and Taylor, G.S. (1994) "Osmotic pump" feeding by coreids. *Entomologia Experimentalis et Applicata* 73, 163–173.

Miller, C.A. (1959) The interaction of the spruce budworm, *Choristoneura fumiferana* (Clem.), and the parasite *Apanteles fumiferanae* Vier. *The Canadian Entomologist* 91, 457–477.

Miller, C.A. (1960) The interaction of the spruce budworm, *Choristoneura fumiferana* (Clem.), and the parasite *Glypta fumiferanae* (Vier.). *The Canadian Entomologist* 92, 839–850.

Miller, C.A. (1966) The black-headed budworm in eastern Canada. *The Canadian Entomologist* 98, 592–613.

Miller, W.E. and Epstein, M.E. (1986) Synchronous population fluctuations among moth species (Lepidoptera). *Environmental Entomology* 15, 443–447.

Mills, N.J. (1982) Voracity, cannibalism and coccinellid predation. *Annals of Applied Biology* 101, 144–148.

Milne, A. (1957a) The natural control of insect populations. *The Canadian Entomologist* 89, 193–213.

Milne, A. (1957b) Theories of natural control of insect populations. *Cold Spring Harbor Symposia on Quantitative Biology* 22, 253–271.

Milne, A. (1962) On a theory of natural control of insect population. *Journal of Theoretical Biology* 3, 19–50.

Milne, A., Laughlin, R. *et al.* (1965) The 1955 and 1959 population crashes of *Tipula paludosa* Meigen. *Journal of Animal Ecology* 34, 529–544.

Milner, M., Kung, K.-J. S. *et al.* (1992) Enhancing overwintering mortality of Colorado potato beetles (Coleoptera: Chrysomelidae) by manipulating the temperature of their diapausing habitat. *Journal of Economic Entomology* 85, 1701–1708.

Mira, A, and Bernays, E.A. (2002) Trade-offs in host use by *Manduca sexta*: plant characters vs natural enemies. *Oikos* 97, 387–397.

Mitchell, P.L. (2004) Heteroptera as vectors of plant pathogens. *Neotropical Entomology* 33, 519–545.

Mitter, C., Farrell, B.D. *et al.* (1991) Phylogenetic studies on insect-plant interactions: insights into the genesis of diversity. *Trends in Ecology and Evolution* 6, 290–293.

Miyatake, T. (2008) Negative relationship between ambient temperature and death-feigning intensity in adult *Callosobruchus maculatus* and *C. chinensis*. *Physiological Entomology* 33, 83–88.

Miyatake, T. and Shimizu, T. (1999) Genetic correlations between life-history and behavioural traits can cause reproductive isolation. *Evolution* 53, 201–208.

Mochida, O. (1975) A strain producing abundant brachypterous adults in *Nilaparvata lugens* (Homoptera: Delphacidae). *Entomologia Experimentalis et Applicata* 18, 465–471.

Moeck, H.A. (1970) Ethanol as the primary attractant for the ambrosia beetle, *Tripodendron lineatum* (Coleoptera: Scolytidae). *The Canadian Entomologist* 102, 11–12.

Mogi, M. (1984) Mosquito problems and their solution in relation to paddy rice production. *Protection Ecology* 7, 219–240.

Mole, S. (1994) Trade-offs and restraints in plant-herbivore defence theory: a life-history perspective. *Oikos* 71, 3–12.

Molyneux, D.H. and Jefferies, D. (1986) Feeding behaviour of pathogen-infected vectors. *Parasitology* 92, 721–736.

Monteith, L.G. (1960) Influence of plants other than the food plants of their host on host-finding by tachinid parasites. *The Canadian Entomologist* 92, 641–652.

Montllor, C.B., Maxmen, A. *et al.* (2002) Facultative bacterial endosymbionts benefit pea aphids *Acyrthosiphon pisum* under heat stress. *Ecological Entomology* 27, 189–195.

Moore, A.J. (1996) The evolution of sexual dimorphism by sexual selection: the separate effects of intrasexual and intersexual selection. *Evolution* 44, 315–331.

Moore, D. and Hunt, D.J. (1987) The role of parasitic nematodes and hymenopterous parasitoids in causing premature death of *Oscinella* spp. larvae. *Annals of Applied Biology* 110, 209–211.

Moore, J.A. (1957) An embryologist's view of the species concept. In: Mayr, E. (ed.) *The Species Problem*. Washington. DC, USA: American Association for the Advancement of Science, pp. 325–338.

Moore, L.V., Myers, J.H. *et al.* (1988) Western tent caterpillars prefer the sunny side of the tree, but why? *Oikos* 51, 321–326.

Moore, R.A. and Singer, M.C. (1987) Effects of maternal age and adult diet on egg weight in the butterfly *Euphydryas editha*. *Ecological Entomology* 12, 401–408.

Moorhouse, E.R., Charnley, A.K. *et al.* (1992) A review of the biology and control of the vine weevil, *Otiorhychus sulcatus* (Coleoptera: Curculionidae). *Annals of Applied Biology* 121, 431–454.

Mopper, S., Beck, M. *et al.* (1995) Local adaptation and agents of selection in a mobile insect. *Evolution* 49, 810–815.

Morales-Ramos, J.A. and Cate, J.R. (1993) Reproductive biology of *Heterospilus megalopus* (Hymenoptera: Braconidae), a parasitoid of *Anthonomus grandis*. *Annals of the Entomological Society of America* 86, 734–739.

Moran, M.D., Rooney, T.P. *et al.* (1996) Top-down cascade from a bitrophic predator in an old-field community *Ecology* 77, 2219–2227.

Moran, N.A. (1992a) The evolutionary maintenance of alternative phenotypes. *The American Naturalist* 139, 971–989.

Moran, N.A. (1992b) The evolution of aphid life cycles. *Annual Review of Entomology* 37, 321–348.

Moran, N.A. (2007) Symbiosis as an adaptive process and source of phenotypic complexity. *Proceedings of the National Academy of Sciences USA* 104, 8627–8633.

Moran, N.A. (2015) Genomics of gut microbial communities in honey bees and bumble bees. *Antenna* (Special Edition), 10–11.

Moran, N.A. and Hamilton, W.D. (1980) Low nutritive quality as a defence against herbivores. *Journal of Theoretical Biology* 86, 247–254.

Moran, N.A. and Whitham, T.G. (1990) Interspecific competition between root-feeding and leaf-galling aphids mediated by host-plant resistance. *Ecology* 71, 1050–1058.

Moran, P.A.P. (1953) The statistical analysis of the Canadian lynx cycle. 2. Synchronisation and meteorology. *Australian Journal of Zoology* 1, 291–298.

Moran, P.A.P. (1964) On the non-existence of adaptive topographies. *Annals of Human Genetics* 27, 383–393.

Moreau, G., Eveleigh, E.S. *et al.* (2006) Ecosystem alteration modifies the relative strengths of bottom-up and top-down forces in a herbivore population. *Journal of Animal Ecology* 75, 853–861.

Moreno, D.S., Sanchez, M. *et al.* (1991) Mating competitiveness of irradiated Mexican fruit flies (Diptera: Tephritidae). *Journal of Economic Entomology* 84, 1227–1234.

Morgan, K.R. and Shelly, T.E. (1988) Body temperature regulation in desert robber flies (Diptera: Asilidae). *Ecological Entomology* 13, 419–428.

Morley, R.J. (2000) *Origin and Evolution of Tropical Rain Forests*. New York, New York, USA: Wiley.

Morrill, W.I., Kushnak, G.D. *et al.* (1994) Wheat stem sawfly (Hymenoptera: Cephidae) damage, rates of parasitism, and overwintering survival in resistant wheat lines. *Journal of Economic Entomology* 87, 1373–1376.

Morris, R.F. (1957) The interpretation of mortality data in studies on population dynamics. *The Canadian Entomologist* 89, 49–69.

Morris, R.F. (1959) Single-factor analysis in population dynamics. *Ecology* 40, 580–588.

Morris, R.F. (1963) (ed.) The dynamics of epidemic spruce budworm populations. *Memoirs of the Entomological Society of Canada* 31, 1–332.

Morris, R.F. (1965) Contemporaneous mortality factors in population dynamics. *The Canadian Entomologist* 97, 1173–1184.

Morris, R.F. (1971) The influence of land use and vegetation on the population density of *Hyphantria cunea*. *The Canadian Entomologist* 103, 1581–1591.

Morris, R.F. (1976) Relation of parasite attack to the colonial habit of *Hyphantria cunea*. *The Canadian Entomologist* 108, 833–836.

Morris, R.F. and Miller, C.A. (1954) The development of life tables for the spruce budworm. *Canadian Journal of Zoology* 32, 283–301.

Morse, D.R., Lawton, J.H. *et al.* (1985) Fractal dimension of vegetation and the distribution of arthropod lengths. *Nature* 314, 731–733.

Morse, J.G. and Zareh, N. (1991) Pesticide-induced hormoligosis of citrus thrips' (Thysanoptera: Thripidae) fecundity. *Journal of Economic Entomology* 84, 1169–1174.

Moser, B.A., Koehler, P.G. *et al.* (1991) Effect of larval diet on cat flea (Siphonaptera: Pulicidae) developmental times and adult emergence. *Journal of Economic Entomology* 84, 1257–1261.

Motro, U. (1983) Optimal rates of dispersal (3). Parent-offspring conflict. *Theoretical Population Biology* 23, 159–168.

Mountford, M.D. (1988) Population regulation, density dependence and heterogeneity. *Journal of Animal Ecology* 57, 845–858.

Mousseau, T.A. and Dingle, H. (1991) Maternal effects in insect life histories. *Annual Review of Entomology* 36, 511–534.

Mueller, L.D. (1997) Theoretical and empirical examination of density-dependent selection. *Annual Review of Ecology and Systematics* 28, 269–288.

Mukerji, M.K. (1971) Major factors in survival of the immature stages of *Hylemya brassicae* (Diptera: Anthomyiidae) on cabbage. *The Canadian Entomologist* 103, 717–728.

Mullen, G. and Durden, L. (2002) *Medical and Veterinary Entomology*. Amsterdam, The Netherlands: Academic Press.

Mullens, B.A. and Peterson, N.G. (2005) Relationship between stable fly (Diptera: Muscidae) abundance on California dairies. *Journal of Medical Entomology* 42, 705–708.

Muller, C.B. and Godfray, H.C.J. (1997) Apparent competition between two aphid species. *Journal of Animal Ecology* 66, 57–64.

Muller, H., Stinson, C.S.A. *et al.* (1989) The entomofaunas of roots of *Centaurea maculosa* Lam., *C. diffusa* Lam. and *C. vallesiaca* Jordan in Europe. *Journal of Applied Entomology* 107, 83–95.

Muller, H.J. (1942) Isolating mechanisms, evolution and temperature. *Biological Symposia* 6, 71–125.

Münster-Swendsen, M. (1991) The effect of sublethal neogregarine infections in the spruce needle miner, *Epinotia tedella* (Lepidoptera: Tortricidae). *Ecological Entomology* 16, 211–219.

Murdoch, W.W. (1966a) Population stability and life history phenomena. *The American Naturalist* 100, 5–11.

Murdoch, W.W. (1966b) Community structure, population control, and competition – a critique. *The American Naturalist* 100, 219–226.

Murdoch, W.W. (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* 39, 335–354.

Murdoch, W.W. (1994) Population regulation in theory and practice. *Ecology* 75, 271–287.

Murdoch, W.W., Chesson, J. *et al*. (1985) Biological control in theory and practice. *The American Naturalist* 125, 344–366.

Murdoch, W.W., Nisbet, R.M *et al.* (1987) An invulnerable age class and stability in delay-differential parasitoid-host models. *The American Naturalist* 129, 263–282.

Murdoch, W.W., Luck, R.F. *et al*. (1995) Regulation of an insect population under biological control. *Ecology* 76, 206–217.

Murdoch, W.W., Swarbrick, S.L. *et al.* (1996) Refuge dynamics and metapopulation dynamics: an experimental test. *The American Naturalist* 147, 424–444.

Murdoch, W.W., Briggs, C.J. *et al*. (1998) Biological control of insects: implications for theory in population ecology. In: Dempster, J.P. and McLean, I.F.G. (eds), *Insect Populations in Theory and Practice*. Dordrecht, Germany: Kluwer Academic Publishers, pp. 167–186.

Murray, B.G. (1979) *Population Dynamics: Alternative Models*. New York, New York, USA: Academic Press.

Murray, B.G. (1988) On measuring individual fitness: a reply to Nur. *Oikos* 51, 249–250.

Murray, B.G. (1994) On density dependence. *Oikos* 69, 520–523.

Murray, B.G. (1999) Can the population regulation controversy be buried and forgotten? *Oikos* 84, 148–152.

Murray, B.G. (2000) Universal laws and predictive theory in ecology and evolution. *Oikos* 89, 403–408.

Murray, J.D. (1989) *Mathematical Biology*. Berlin, Germany: Springer.

Murrell, D.J., Travis, J.M.J. *et al.* (2002) The evolution of dispersal distance in spatially structured populations. *Oikos* 97, 229–236.

Murthy, C.S.H.N. (1983) Effect of pesticides on photosynthesis. *Residue Reviews* 86, 107–129.

Musser, F., Stewart, S. (2007) Comparison of direct and indirect sampling methods for tarnished plant bugs (Hemiptera: Miridae) in flowering cotton. *Journal of Economic Entomology* 100, 1916–1923.

Muthukrishnan, J., Marian, M.P. *et al.* (1983) Population dynamics in relation to breeding of the wasp *Sceliphron violaceum* and its parasitoid *Melittobia* sp. *Entomon* 8, 115–122.

Myers, J.H. (1980) Is the insect or the plant the driving force in the cinnabar moth-tansy ragwort system? *Oecologia* 23, 255–269.

Myers J.H. (1985) Effect of physiological condition of the host plant on the ovipositional choice of the cabbage white butterfly, P. rapae. *Australian Journal of Ecology* 54, 193–204.

Myers, J.H. (1988) Can a general hypothesis explain population cycles in forest Lepidoptera? *Advances in Ecological Research* 18, 179–242.

Myers, J.H. (1998) Synchrony in outbreaks of forest Lepidoptera: a possible example of the Moran effect. Ecology 79, 1111–1117.

Myers, J.H., Boettner, G. *et al.* (1998a) Maternal effects in gypsy moth: only sex-ratio varies with population density. *Ecology* 79, 305–314.

Myers, J.H., Savoie, A. *et al.* (1998b) Eradication and pest management. *Annual Review of Entomology* 43, 471–491.

Myers, N., Mittermeier, R.A. *et al.* (2000) Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.

Nagel, E. and Newman, J. (2008) *Gödel's Proof*. New York, New York, USA: New York University Press.

Nair, K.S.S. (2007) *Tropical Forest Insect Pests*. Cambridge, UK: Cambridge University Press.

Nakamura, M., Utsumi, S. *et al.* (2005) Flood initiates bottom-up cascades in a tri-trophic system: host plant regrowth increases densities of a leaf beetle and its predators. *Journal of Animal Ecology* 74, 683–691.

Nakasuji, F., Yamanaka, H. *et al.* (1973) The disturbing effect of micryphantid spiders on the larval aggregation of the tobacco cutworm *Spodoptera litura.* (Lepidoptera: Noctuidae). *Kontyu* 41, 220–227.

Nalepa, C.A. (2015) Origin of termite eusociality: trophallaxis integrates the social, nutritional and microbial environments. *Ecological Entomology* 40, 323–335.

Nansen, C., Macedo, T.B. *et al.* (2005) Spatiotemporal distributions of wheat stem sawfly eggs and larvae in dryland wheat fields. *The Canadian Entomologist* 137, 428–440.

Nansen, C., Meikle, W.G. *et al.* (2008) A binomial and species-independent approach to trap capture analysis of flying insects. *Journal of Economic Entomology* 101, 1719–1728.

Nascimento, M.T. and Proctor, J. (1994) Insect defoliation of a monodominant Amazonian rainforest. *Journal of Tropical Ecology* 10, 633–636.

Nash, D.R., Agassiz, D.J.L. *et al.* (1995) The pattern of spread of invading species: two leaf-mining moths colonising Great Britain. *Journal of Animal Ecology* 64, 225–233.

Nault, L.R. (1997) Arthropod transmission of plant viruses: a new synthesis. *Annals of the Entomological Society of America* 90, 521–541.

Nealis, V.G. and Lomic, P.V. (1994) Host-plant influence on the population ecology of the jack pine budworm, *Choristoneura pinus* (Lepidoptera: Tortricidae). *Ecological Entomology* 19, 367–373.

Nealis, V.G. and Regniere, J. (2004) Fecundity and recruitment of eggs during outbreaks of the spruce budworm. *The Canadian Entomologist* 136, 591–604.

Nealis, V.G. and Regniere, J. (2016) Why western spruce budworms travel so far for the winter. *Ecological Entomology* 41, 633–641.

Nedvěd, O. and Honěk, A. (2012) Life history and development. In: Hodek, I., van Emden, H.F. *et al.* (eds) *Ecology and Behaviour of the Ladybird Beetles*. Oxford, UK: Blackwell, pp. 54–109.

Nei, M., Maruyama, T. *et al.* (1975) The bottleneck effect and genetic variability in populations. *Evolution* 29, 1–10.

Neiman, M. and Taylor, D.R. (2009) The causes of mutation accumulation in mitochondrial genomes. *Proceedings of the Royal Society B* 276, 1201–1209.

Nelson, E.H. and Rosenheim, J.A. (2006) Encounters between aphids and their predators: the relative frequencies of disturbance and consumption. *Entomologia Experimentalis et Applicata* 118, 211–219.

Nelson, E.H., Matthews, C.E. *et al.* (2004) Predators reduce population growth by inducing changes in prey behavior. *Ecology* 85, 1853–1858.

Nelson, W.A. (1953) Observations on hyperparasitism in the wheat stem sawfly *Cephus cinctus* Nort. (Hymenoptera: Cephidae). *The Canadian Entomologist* 85, 249–251.

Nestel, D., Dickschen, F. *et al.* (1994) Seasonal and spatial population loads of a tropical insect: the case of the coffee leaf-miner in Mexico. *Ecological Entomology* 19, 159–167.

Nettles, W.C. (1987) *Eucelatoria bryani* (Diptera: Tachinidae): effect on fecundity of feeding on hosts. *Environmental Entomology* 16, 437–440.

Neven, L.G. (2004) Effects of low temperature on egg and larval stages of the lesser appleworm. *Journal of Economic Entomology* 97, 820–823.

Nevo, E. (1983) Population genetics and ecology: the interface. In: Bendall, D.S. (ed.) *Evolution from Molecules to Men*. Cambridge, UK: Cambridge University Press.

Neyman, J. (1939) On a new class of “contagious” distributions applicable to entomology and bacteriology. *Annals of Mathematical Statistics* 10, 35–57.

Ngeve, J.M. (2003) Cassava root yields and culinary qualities as affected by harvest age and test environment. *Journal of the Science of Food and Agriculture* 83, 249–257.

Nguyen, C. (2003) Rhizodeposition of organic C by plants: mechanisms and controls. *Agronomie* 23, 375–396.

Nicholle, C., Compte, C. *et al.* (1909) Transmission expérimentale du typhus exanthèmatique par le pou du corps. *Compte Rendu de l’Académie des Sciences, Paris* 149, 486–489.

Nicholson, A.J. (1933) The balance of animal populations. *Journal of Animal Ecology* 2, 132–178.

Nicholson, A.J. (1954) An outline of the dynamics of animal populations. *Australian Journal of Zoology* 2, 9–65.

Nicholson, A.J. (1958) Dynamics of insect populations. *Annual Review of Entomology* 3, 107–136.

Nicholson, A.J. (1959) Density-dependent factors in ecology. *Nature* 183, 911–912.

Nicholson, A.J. and Bailey, V.A. (1935) The balance of animal populations. *Proceedings of the Zoological Society of London* 3, 551–598.

Nicolai, V. (1986) The bark of trees: thermal properties, microclimate and fauna. *Oecologia* 69, 148–160.

Nielsen, B.O. and Ejlersen, A. (1977) The distribution pattern of herbivory in a beech canopy. *Ecological Entomology* 2, 293–299.

Nielsen, D.G and Dunlap, M.J. (1981) Black vine weevil: reproductive potential on selected plants. *Annals of the Entomological Society of America* 74, 60–65.

Nielsen, E.T. (1961) On the habits of the migratory butterfly *Ascia monuste* L. *Biologiske Meddelelser* 23, 1–81.

Niemala, P. and Haukioja, E. (1982) Seasonal patterns of species richness of herbivores: macrolepidopteran larvae on Finnish deciduous trees. *Ecological Entomology* 7, 169–175.

Niemela, P. and Mattson, W.J. (1996) Invasion of North American forests by European moths. *Bioscience* 46, 741–753.

Nieminen, M. and Hanski, I. (1998) Metapopulations of moths on islands: a test of two contrasting models. *Journal of Animal Ecology* 67, 149–160.

Nigam, Y., Dudley, E. *et al.* (2010) The physiology of wound healing by the medicinal maggot, *Lucilia sericata*. *Advances in Insect Physiology* 39, 39–81.

Nikam, P.K. and Pawar, C.V. (1993) Life tables and intrinsic rate of natural increase of *Bracon hebetor* Say (Hym.: Braconidae) population on *Corcyra cephalonica* Staint. (Lep.: Pyralidae), a key parasitoid of *Helicoverpa armigera* Hbn. (Lep.: Noctuidae) *Journal of Applied Entomology* 115, 210–213.

Niklas, K.J. (1985) Wind pollination: a study in controlled chaos. *American Scientist* 73, 462–470.

Nikpay, A. (2007) Insecticidal effect of spinosad dust against four stored product insect species in different grain commodities. *International Journal of Pest Management* 53, 121–125.

Normark, B.B. (2003) The evolution of alternative genetic systems in insects. *Annual Review of Entomology* 48, 397–423.

Norrbom, A.L. and Korytkowski, C.A. (2009) A revision of the *Anastrepha robusta* species group (Diptera: Tephritidae). *Zootaxa* 2182, 1–91.

Norris, K.R. (1965) The bionomics of blow flies. *Annual Review of Entomology* 10, 47–68.

Novotny, V. (1994) Association of polyphagy in leafhoppers (Auchenorrhyncha: Hemiptera) with unpredictable environments. *Oikos* 70, 223–232.

Novotny, V., Drozd, P. *et al.* (2006) Why are there so many species of herbivorous insects in tropical rain forests? *Science* 313, 1115–1118.

Noyes, J.S. (2011) Universal Chalcidoidea database. Available at: https://www.nhm.ac.uk/our-science/data/chalcidoids/database/ (accessed 18 June 2020).

Nur, U., Werren, J.H. *et al.* (1988) A “selfish” B chromosome that enhances its transmission by eliminating the paternal genome. *Science* 240, 512–514.

Nuttman, C. and Willmer, P.G. (2003) How does insect visitation trigger floral colour change? *Ecological Entomology* 28, 467–474.

Nyabuga, F.N., Loxdale, H.D. *et al.* (2010) Spatial population dynamics of a specialist aphid parasitoid, *Lysiphlebus hirticofnis* Mackauer (Hymenoptera: Braconidae: Aphidiinae): evidence for philopatry and restricted dispersal. *Heredity* 105, 433–442.

Nye, P.H. (1961) Organic matter and nutrient cycles under moist tropical forest. *Plant and Soil* 8, 333–346.

Nylin, S. and Gotthard, K. (1998) Plasticity in life-history traits. *Annual Review of Entomology* 43, 63–83.

Öberg, S. and Ekbom, B. (2006) Recolonisation and distribution of spiders and carabids in cereal fields after spring sowing. *Annals of Applied Biology* 149, 203–211.

Oberhauser, K.S. (1997) Fecundity, life-span and egg mass in butterflies: effects of male-derived nutrients and female size. *Functional Ecology* 11, 166–175.

O’Brien, D.M. (1999) Fuel use in flight and its dependence on nectar feeding in the hawk moth *Amphion floridensis*. *The Journal of Experimental Biology* 202, 441–451.

O’Brien, M. and Mullins, E. (2009) Relevance of genetically modified crops in the light of future environmental and legislative challenges to the agri-environment. *Annals of Applied Biology* 154, 323–340.

O’Brien, M., Spillane, C. *et al.* (2008) An insight into the impact of arable farming on Irish biodiversity: a scarcity of studies hinders a rigorous assessment. *Biology and Environment: Proceedings of the Royal Irish Academy* 108B, 97–108.

Obrycki, J.J. and Kring, T.J. (1998) Predaceous Coccinellidae in biological control. *Annual Review of Entomology* 43, 375–405.

Occam,W. (1324) *Summa Logicae Paris Prima*. Bochner, P. (ed.) New York and Louvain: Franciscan Institute.

O'Connor, J.P. and Malumphy, C. (2011) A review of the Irish jumping plant-lice (Hemiptera: Psylloidea). *Bulletin of the Irish Biogeographical Society* 35, 21–63.

Ode, P.J. (2006) Plant chemistry and natural enemy fitness: effects on herbivore and natural enemy interactions. *Annual Review of Entomology* 51, 163–185.

Odiyo, P.O. (1979) Forecasting infestations of a migrant pest: the African armyworm *Spodoptera exempta* (Walk.) *Philosophical Transactions of the Royal Society B* 287, 403–413.

Odum, E.P. (1971) *Fundamentals of Ecology*, 3rd edn. Philadelphia, Pennsylvania, USA: Saunders.

Oerke, E.-C. (2006) Crop losses to pests. *Journal of Agricultural Science* 144, 31–43.

Ofomata, V.C., Overholt, W.A. *et al*. (1999) Niche overlap and interspecific association between *Chilo partellus* and *Chilo orichalcociliellus* on the Kenya coast. *Entomologia Experimentalis et Applicata* 93, 141–148.

Ogol, C.K.P.O. and Spence, J.R. (1997) Abundance, population dynamics and impact of the leucaena psyllid *Heteropsylla cubana* Crawford in a maize-leucaena agroforestry system in Kenya. *Insect Science and its Application* 17, 182–192.

O'Hara, R.B. (2005) Comparing the effects of genetic drift and fluctuating selection on genotype frequency changes in the scarlet tiger moth. *Proceedings of the Royal Society B* 272, 211–217.

Ohgushi, T. (1996) Consequences of adult size for survival and reproductive performance in a herbivorous ladybird beetle. *Ecological Entomology* 21, 47–55.

Ohgushi, T. (1998) Bottom-up population regulation in a herbivorous lady beetle: an evolutionary perspective. In: Dempster, J.P. and McLean, I.F.G. (eds) *Insect Populations in Theory and Practice*. Dordrecht, Germany: Kluwer Academic Publishers, pp. 367–389.

Ohgushi, T. (2005) Indirect interaction webs: herbivore-induced effects through trait change in plants. *Annual Review of Ecology, Evolution and Systematics* 36, 81–105.

Ohgushi, T. (2008) Herbivore-induced indirect interaction webs on terrestrial plants: the importance of non-trophic, indirect, and facultative interactions. *Entomologia Experimentalis et Applicata* 128, 217–229.

Ohsaki, N. and Sato, Y. (1990) Avoidance mechanisms by three *Pieris* butterfly species against the parasitoid *Apanteles glomeratus*. *Ecological Entomology* 15, 169–176.

Ohsaki, N. and Sato, Y. (1994) Food plant choice of Pieris butterflies as a trade-off between parasitoid avoidance and quality of plants. *Ecology* 75, 59–68.

Okeyo-Owuor, J.B. and Oloo, G.W. (1991) Life tables, key factor analysis and density relations in natural populations of the legume pod borer *Maruca testulalis* Geyer (Lepidoptera: Pyralidae) in western Kenya. *Insect Science and its Application* 12, 423–431.

Oksanen, L. (1991) A century of community ecology: how much progress? *Trends in Ecology and Evolution* 6, 294–296.

Okubo, A. and Levin, S.A. (1989) A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* 70, 329–338.

Oldroyd, H. (1964) *The Natural History of Flies*. London, UK: Weidenfeld and Nicolson.

Olfert, O., Doane, J.F. *et al*. (2003) Establishment of *Platygaster tuberosula*, an introduced egg parasitoid of the wheat midge *Sitodiplosis mosellana*. *The Canadian Entomologist* 135, 303–308.

Olfert, O., Woods, S. *et al*. (2004) Potential distribution and relative abundance of an invasive cereal crop pest, *Oulema melanopus* (Coleoptera: Chrysomelidae), in Canada. *The Canadian Entomologist* 136, 277–287.

Oliver, J.C., Robertson, K.A. *et al*. (2009) Accommodating natural and sexual selection in butterfly wing pattern evolution. *Proceedings of the Royal Society B* 276, 2369–2375.

Oliver, K.M., Campos, J. *et al*. (2008) Population dynamics of defensive symbionts in aphids. *Proceedings of the Royal Society B* 275, 293–299.

Olofsson, E. (1986) Effects of feeding by *Neodiprion sertifer* (Fourcroy) (Hymenoptera: Diprionidae) on frost resistance in Scots pine shoots and mortality of larvae caused by frost. *Journal of Applied Entomology* 102, 101–106.

Olson, J.G., Reeves, W.C. *et al*. (1979) Correlation of *Culex tarsalis* population indices with the incidence of St. Louis encephalitis and western equine encephalomyelitis in California. *American Journal of Tropical Medicine* 28, 335–343.

Omacini, M., Chaneton, E.J. *et al*. (2001) Symbiotic fungal endophytes control insect host-parasite interaction webs. *Nature* 409, 78–81.

Ondiaka, S., Maniania, N.K. *et al.* (2008) Virulence of the entomopathogenic fungi *Beauveria bassiana* and *Metarhizium anisopliae* to sweet potato weevil *Cylas puncticollis* and effects on fecundity and egg viability. *Annals of Applied Biology* 153, 41–48.

Ooi, P.A.C. (1996) Experiences in educating rice farmers to understand biological control. *Entomophaga* 41, 375–385.

Opit, G.P. and Throne, J.E. (2008) Population growth and development of the psocid *Lepinotus reticulatus* at constant temperatures and relative humidities. *Journal of Economic Entomology* 101, 605–615.

Opler, P.A. (1974) Oaks as evolutionary islands for leaf-mining insects. *American Scientist* 62, 67–73.

Orians, C.M. and Jones, C.G. (2001) Plants as resource mosaics: a functional model for predicting patterns of within-plant resource heterogeneity to consumers, based on vascular architecture and local environmental variability. *Oikos* 94, 493–504.

Orr, H.A. (1996) Dobzhansky, Bateson, and the genetics of speciation. *Genetics* 144, 1331–1335.

Orr, H.A. (1997) Haldane's rule. *Annual Review of Ecology and Systematics* 28, 195–218.

Orr, H.A, (2000) Adaptation and the cost of complexity. *Evolution* 54, 13–20.

Orwell, G. (1938) *Homage to Catalonia*. London, UK: Secker and Warburg.

Osbourne, P.J. (1969) An insect fauna of late Bronze Age date from Wilsford, Wiltshire. *Journal of Animal Ecology* 38, 555–566.

Ossiannilsson, F. (1966) Insects in the epidemiology of plant viruses. *Annual Review of Entomology* 11, 213–232.

Otranto, D., Colwell, D.D. *et al.* (2005) *Hypoderma sinense*: solving a century-old enigma. *Medical and Veterinary Entomology* 19, 315–321.

Otte, D. and Joern, A. (1975) Insect territoriality and its evolution: population studies of desert grasshoppers on creosote bushes. *Journal of Animal Ecology* 44, 29–54.

Otvos, I.S. (1965) Studies on avian predators of *Dendroctonus brevicornis* LeConte (Coleoptera: Scolytidae) with special reference to Picidae. *The Canadian Entomologist* 97, 1184–1199.

Outram, I. (1971) Aspects of mating in the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *The Canadian Entomologist* 103, 1121–1127.

Ovaskainen, O. and Hanski, I. (2004) From individual behavior to metapopulation dynamics: unifying the patchy population and classic metapopulation models. *The American Naturalist* 164, 364–377.

Overhulser, D., Gara, R.I. *et al.* (1972) Emergence of *Pissodes strobi* (Coleoptera: Curculionidae) from previously attacked Sitka spruce. *Annals of the Entomological Society of America* 65, 1423–1424.

Ovington, J.D. (1962) Quantitative ecology and the woodland ecosystem concept. *Advances in Ecological Research* 1, 103–192.

Ovruski, S.M. (1995) Pupal and larval-pupal parasitoids (Hymenoptera) obtained from *Anastrepha* spp. and *Ceratitis capitata* (Dipt.: Tephritidae) pupae collected in four localities of Tucuman province, Argentina. *Entomophaga* 40, 367–370.

Owen, D.F. (1980). How plants may benefit from the animals that eat them. *Oikos* 35, 230–235.

Owen, D.F. and Owen, J. (1974) Species diversity in temperate and tropical Ichneumonidae. *Nature* 249, 583–584.

Packer, M.J. and Corbet, P.S. (1989) Seasonal emergence, host-seeking activity, age composition and reproductive biology of the mosquito *Aedes punctor*. *Ecological Entomology* 14, 433–442.

Paige, K.N. and Whitham, T.G. (1987) Overcompensation in response to mammalian herbivory: the advantage of being eaten. *The American Naturalist* 129, 407–416.

Pair, S.D., Bruton, B.D. *et al.* (2004) Overwintering squash bugs harbor and transmit the causal agent of cucurbit yellow vine disease. *Journal of Economic Entomology* 97, 74–78.

Panassiti, B, Breuer, M. *et al.* (2013) Influence of environment and climate on occurrence of the cixiid planthopper *Hyalesthes obsoletus*, the vector of the grapevine disease "bois noir". *Bulletin of Entomological Research* 103, 621–633.

Panayotou, T. and Ashton, P.S. (1992) *Not by Timber Alone: Economics and Ecology for Sustaining Tropical Forests*. Washington, DC, USA: Island.

Pantel, J. (1910) Recherches sur les Dipteres a larves entomobies I. Characteres parasitiques aux points de vue biologique, ethologique et histologique. *La Cellule* 26, 27–216.

Papaj, D.R. and Lewis, A.C. (eds) (1993) *Insect Learning. Ecology and Evolutionary Perspectives*. New York, New York, USA: Chapman and Hall.

Parish, W.E.G. and Bale, J.S. (1991) Effect of low temperature on the intracellular symbionts of the grain aphid *Sitobion avenae* (F.) (Hem. Aphididae). *Journal of Insect Physiology* 37, 339–345.

Park, T. (1954) Experimental studies on interspecies competitions, 2. Temperature, humidity and competition in two species of *Tribolium*. *Physiological Zoology* 27, 177–238.

Park, T. (1962) Beetles, competition, and populations. *Science* 138, 1369–1375.

Parker, F.D. and Pinnell, R.E. (1973) Effect of food consumption of the imported cabbageworm when parasitized by two species of *Apanteles*. *Environmental Entomology* 2, 216–219.

Parker, G.A. (1970) Sperm competition and its evolutionary consequences in the insects. *Biological Reviews* 45, 525–567.

Parker, G.A. (1978) Evolution of competitive mate searching. *Annual Review of Entomology* 23, 173–196.

Parker, G.A. (1992) Snakes and female sexuality. *Nature* 355, 395–396.

Parker, V.T. (2004) The community of an individual: implications for the community concept. *Oikos* 104, 27–34.

Parmesan, C. (1996) Climate and species' range. *Nature* 382, 765–766.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* 37, 637–669.

Parmesan, C., Ryrholm, N. *et al*. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399, 579–583.

Parry, D., Spence, J.R. *et al*. (1997) Responses of natural enemies to experimentally increased populations of the forest tent caterpillar, *Malacosoma disstria*. *Ecological Entomology* 22, 97–108.

Pascual, M. and Levin, S. (1999) From individuals to population densities: searching for the intermediate scale of non-trivial determinism. *Ecology* 80, 2225–2236.

Paterson, H.E.H. (1980) A comment on "Mate Recognition Systems". *Evolution* 34, 330–331.

Paterson, H.E.H. (1982) Perspective on speciation by reinforcement. *South African Journal of Science* 78, 53–57.

Pates, H. and Curtis, C. F. (2005) Mosquito behavior and vector control. *Annual Review of Entomology* 50, 53–70.

Patten, B.C. (1961) Competitive exclusion. *Science* 134, 1599–1601.

Pavlyuchuk, M.V. (1969) *Opomyza* – a pest of winter cereals. *Zashchita restenii* 14, 24–25.

Pearce, D., Hecht, S. *et al*. (2007) What is biodiversity worth? Economics as a problem and a solution. In: Macdonald, D.W. and Service, K. (eds) *Key Topics in Conservation Biology*. Oxford, UK: Blackwell Publishing.

Pearl, R., Park, T. *et al*. (1941) Experimental studies on the duration of life. 16. Life tables for the flour beetle *Tribolium confusum* Duval. *The American Naturalist* 75, 5–19.

Pearsall, I.A. and Walde, S.J. (1994) Parasitism and predation as agents of mortality in winter moth populations in neglected apple orchards in Nova Scotia. *Ecological Entomology* 19, 190–198.

Pearson, D.L. (1985) The function of multiple antipredator mechanisms in adult tiger beetles (Coleoptera: Cicindelidae). *Ecological Entomology* 10, 65–72.

Pearson, D.L. (1988) Biology of tiger beetles. *Annual Review of Entomology* 33, 123–147.

Pearson, D.L. and Knisley, C.B. (1985) Evidence for food as a limiting resource in the life cycle of tiger beetles (Coleoptera: Cicindelidae). *Oikos* 45, 161–168.

Peccoud, J., and Simon, J-C. (2010) The pea aphid complex as a model of ecological speciation. *Ecological Entomology* 35 (Suppl.), 119–130.

Pedgley, D.E. (1982) *Windborne Pests and Diseases*. Chichester, UK: Ellis Horwood.

Pedgley, D.E. (1990) Concentration of flying insects by the wind. *Philosophical Transactions of the Royal Society B* 328, 631–653.

Pedgley, D.E., Reynolds, D.R. *et al*. (1995) Long-range insect migration in relation to climate and weather: Africa and Europe. In: Drake, V.A. and Gatehouse, A.G. (eds) *Insect Migration: Tracking Resources Through Space and Time*. Cambridge, UK: Cambridge University Press, pp. 3–29.

Pedigo, L.P. (1996) *Entomology and Pest Management*, 4th edn. Upper Saddle River, New Jersey, USA: Prentice-Hall.

Pedigo, L.P. (2002) *Entomology and Pest Management*, 4th edn. Upper Saddle River, New Jersey, USA: Prentice-Hall.

Pener, M.P. (1991) Locust phase polymorphism and its endocrine relations. *Recent Advances in Insect Physiology* 22, 1–79.

Pener, M.P. and Simpson, S.J. (2009) Locust phase polyphenism: an update. *Advances in Insect Physiology* 36, 1–286.

Penev, L.D. (1992) Qualitative and quantitative spatial variation in soil wire-worm assemblages in relation to climatic and habitat factors. *Oikos* 63, 180–192.

Pennacchio, F. and Strand, M.R. (2006) Evolution of developmental strategies in parasitic Hymenoptera. *Annual Review of Entomology* 51, 233–258.

Pennisi, E. (2001) Malaria's beginnings: on the heels of hoes? *Science* 293, 416–417.

Pérez, J., Infante, F. *et al.* (2005) Does the coffee berry borer (Coleoptera: Scolytidae) have mutualistic fungi? *Annals of the Entomological Society of America* 98, 483–490.

Pérez, J., Rojas, J.C. *et al.* (2013) *Anastrepha* egg deposition induces volatiles in fruits that attract the parasitoid *Fopius aristanus*. *Bulletin of Entomological Research* 103, 318–325.

Perfectti, F. and Werren, J.H. (2001) The interspecific origin of B chromosomes: experimental evidence. *Evolution* 55, 1069–1073.

Perring, T.M. (2001) The *Bemisia tabaci* species complex. *Crop Protection* 20, 725–737.

Perry, D.A. (1998) The scientific basis of forestry. *Annual Review of Ecology and Systematics* 29, 435–466.

Persig, R.M. (1974) *Zen and the Art of Motor Cycle Maintenance*. London, UK: The Bodley Head.

Peterson, C.J., Carson, W.P. *et al.* (1990) Microsite variation and soil dynamics within newly created treefall pits and mounds. *Oikos* 58, 39–46.

Peterson, R.K.D., Davis, R.S. *et al.* (2009) Mortality risk in insects. *Environmental Entomology* 38, 2–10.

Petit, R.J. and Excoffier, L. (2009) Gene flow and species delimitation. *Trends in Ecology and Evolution* 24, 386–393.

Petit, S., Moilanen, A. *et al.* (2001) Metapopulation dynamics of the bog fritillary butterfly: movement between habitat patches. *Oikos* 92, 491–500.

Phillipson, J. and Thompson, D.J. (1983) Phenology and intensity of phyllophage attack on *Fagus sylvatica* in Wytham Woods, Oxford. *Ecological Entomology* 8, 315–330.

Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of the concepts. *The American Naturalist* 100, 33–46.

Pianka, E.R. (1972) *r*- and *K*-selection or *b*- and *d*-selection? *The American Naturalist* 106, 581–588.

Pianka, E.R. (1976) Competition and niche theory. In: May, R.M. (ed.) *Theoretical Ecology: Principles and Applications*. Philadelphia, Pennsylvania, USA: Saunders, pp. 114–143.

Pichon, A., Arvanitakis, L. *et al.* (2006) Genetic differentiation among various populations of the diamondback moth, *Plutella xylostella* (Lepidoptera: Yponomeutidae). *Bulletin of Entomological Research* 96, 137–144.

Pielou, E.C. (1966) Species-diversity and pattern-diversity in the study of ecological succession. *Journal of Theoretical Biology* 10, 370–383.

Pielou, E.C. (1975) *Ecological Diversity*. New York, New York, USA: Wiley-Interscience.

Pielou, E.C. (1981) The usefulness of ecological models: a stocktaking. *The Quarterly Review of Biology* 56, 17–31.

Pijls, J.W.A.M. and van Alphen, J.J.M (1996) On the coexistence of the cassava mealybug parasitoids *Apoanagryrus diversicornis* and *A. lopezi* (Hymenoptera: Encyrtidae) in their native South America. *Bulletin of Entomological Research* 86, 51–59.

Pimentel, D. (1961) Species diversity and insect population outbreaks. *Annals of the Entomological Society of America* 54, 76–86.

Pimentel, D. (1968) Population regulation and genetic feedback. *Science* 159, 1432–1437.

Pimentel, D., Glenister, C. *et al.* (1984) Environmental risks of biological pest controls. *Oikos* 42, 283–290.

Pimm, S.L. (1984) The complexity and stability of ecosystems. *Nature* 307, 321–326.

Pimm, S.L. and Lawton, J.H. (1977) Number of trophic levels in ecological communities. *Nature* 268, 329–331.

Pimm, S.L. and Redfearn, A. (1988) The variability of natural populations. *Nature* 334, 613–614.

Pinder, J.E., Wiener, J.G. *et al.* (1978) The Weibull distribution: a new method of summarising survivorship data. *Ecology* 59, 175–179.

Platt, J.R. (1964) Strong inference. *Science* 146, 347–353.

Plowes, R.M., Lebrun, E.G. *et al.* (2009) A review of *Pseudacteon* (Diptera: Phoridae) that parasitize ants of the *Solenopsis geminata* complex (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* 102, 937–958.

Podoler, H. and Rogers, D. (1975) A new method for the identification of key factors from life-table data. *Journal of Animal Ecology* 44, 85–114.

Poelman, E.H., Oduor, A.M.O. *et al.* (2009) Field parasitism rates of caterpillars on Brassica oleracea plants are reliably predicted by differential attraction of Cotesia parasitoids. *Functional Ecology* 23, 951–962.

Polis, G.A. (1981) The evaluation and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics* 12, 225–251.

Polis, G.A. (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* 86, 3–15.

Polis, G.A. and Strong, D.R. (1996) Food web complexity and community dynamics. *The American Naturalist* 147, 813–846.

Polis, G.A., Myers, C.A. *et al.* (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20, 297–330.

Polis, G.A., Hurd, S.D. *et al.* (1997a) El Niño effects on the dynamics and control of a terrestrial island ecosystem in the Gulf of California. *Ecology* 78, 1884–1897.

Polis, G.A., Anderson, W.B. *et al.* (1997b) Toward an integration of landscape and food web ecology. *Annual Review of Ecology and Systematics* 28, 289–316.

Polivka, J.B. (1960) Grub populations in turf areas with pH levels in Ohio soils. *Journal of Economic Entomology* 53, 860–863.

Pollard, E. (1979) Population ecology and change in range of the white admiral butterfly *Ladoga camilla* L. in England. *Ecological Entomology* 4, 61–74.

Pollard, E. (1991) Synchrony of population fluctuations: the dominant influence of widespread factors on local butterfly populations. *Oikos* 60, 7–10.

Pollard, E. and Rothery, P. (1994) A simple stochastic model of resource-limited insect populations. *Oikos* 69, 289–294.

Pollard, E., Lakhani, K.H. *et al.* (1987) The detection of density dependence from a series of annual censuses. *Ecology* 68, 2046–2055.

Popham, E.J. (1942) Further experimental studies of the selective action of predators. *Proceedings of the Zoological Society of London* 112, 105–117.

Popov, G.B. (1965) *Review of the work of the Desert Locust Ecological Survey 1958–1964*. FAO Report No. UNSF/DL/ES/8. Rome, Italy: Food and Agriculture Organization of the United Nations.

Popper, K.R. (1989) *Conjectures and Refutations*, 5th edn. London, UK: Routledge.

Poprawski, T.J., Robert, P.H. *et al.* (1985) Susceptibility of *Delia antiqua* (Diptera: Anthomyiidae) to eleven isolates of entomopathogenic Hyphomycetes. *Environmental Entomology* 14, 557–561.

Posey, F.R., White, W.H. *et al.* (2006) Sugarcane borer (Lepidoptera: Crambidae) management threshold assessment on four sugarcane cultivars. *Journal of Economic Entomology* 99, 966–971.

Potter, D.A. and Held, D.W. (2002) Biology and management of Japanese beetles. *Annual Review of Entomology* 47, 175–205.

Potts, G.R. (1990) The environmental and ecological importance of cereal fields. In: Firbank, L.G., Carter, N. *et al.* (eds) *The Ecology of Temperate Cereal Fields*. London, UK: Blackwell, pp. 3–21.

Poulton, E.B. (1887) An inquiry into the cause and extent of a special colour-relation between certain exposed lepidopterous pupae and the surface which immediately surrounds them. *Proceedings of the Royal Society* 42, 94–108.

Poulton, E.B. (1904) What is a species? *Proceedings of the Entomological Society of London* 1903, 77–94.

Powell, D. (1938) The biology of *Cephalonomia tarsalis* (Ash.), a vespoid wasp (Bethylidae: Hymenoptera) parasitic on the saw-toothed grain beetle. *Annals of the Entomological Society of America* 31, 44–49.

Powell, W. (1986) Enhancing parasitoid activity in crops. In: Waage, J.K. and Greathead, D.J. (eds) *Insect Parasitoids*. London, UK: Academic Press, pp. 319–340.

Powell, W. and Wright, A.F. (1988) The abilities of the aphid parasitoids *Aphidius ervi* Haliday and *A. rhopalosiphi* De Stephani Perez (Hymenoptera: Braconidae) to transfer between different known host species and the implications for the use of alternative hosts in pest control strategies. *Bulletin of Entomological Research* 78, 683–693.

Pratissoli, D. and Parra, J.R.P. (2000) Fertility life table of *Trichogramma pretiosum* (Hym., Trichogrammatidae) in eggs of *Tuta absoluta* and *Phthorimaea operculella* (Lep., Gelechiidae) at different temperatures. *Journal of Applied Entomology* 124, 339–342.

Prebble, J. (1990) *The Highland Clearances*. London, UK: Penguin Books.

Prebble, M.L. (1975) *Aerial control of forest insects in Canada*. Ottawa, Canada: Department of Environment.

Preisser, E.L., Bolnick, D.I. *et al.* (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86, 501–509.

Preston, F.W. (1962) The canonical distribution of commonness and rarity. *Ecology* 43, 185–215, 410–432.

Preston, F.W. (1980) Noncanonical distributions of commonness and rarity. *Ecology* 61, 88–97.

Preszler, R.W. and Price, P.W. (1988) Host quality and sawfly populations: A new approach to life table analysis. *Ecology* 69, 2012–2020.

Price, G.R. (1972) Fisher's "fundamental theorem" made clear. *Annals of Human Genetics* 36, 129–140.

Price, M.V. and Waser, N.M. (1979) Pollen dispersal and optimal outcrossing in *Delphinium nelsoni*. *Nature* 277, 294–296.

Price, P.W. (1973) Reproductive strategies in parasitoid wasps. *The American Naturalist* 107, 684–693.

Price, P.W. (1980) *Evolutionary Biology of Parasites*. Princeton, New Jersey, USA: Princeton University Press.

Price, P.W. (1984) *Insect Ecology*, 2nd edn. New York, New York, USA: Wiley.

Price, P.W. (1988) Inversely density-dependent parasitism: the role of plant refuges for hosts. *Journal of Animal Ecology* 57, 89–96.

Price, P.W. (1991) The plant vigour hypothesis and herbivore attack. *Oikos* 62, 244–251.

Price, P.W. (1992) Resource-based organization of communities. *Biotropica* 24, 273–282.

Price, P.W. (1997) *Insect Ecology*, 3rd edn. New York, New York, USA: Wiley.

Price, P.W. and Hunter, M.D. (2005) Long-term population dynamics of a sawfly show strong bottom-up effects. *Journal of Animal Ecology* 74, 917–925.

Price, P.W. and Pschorn-Walcher, H. (1988) Are galling insects better protected against parasitoids than exposed feeders?: a test using tenthredinid sawflies. *Ecological Entomology* 13, 195–205.

Price, P.W., Bouton, C.E. *et al.* (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* 11, 41–65.

Price, P.W., Craig, T.P. *et al.* (1998) Population ecology of a gall-inducing sawfly, *Euura lasiolepis*, and relatives. In: Dempster, J.P. and McLean, I.F.G. (eds) *Insect Populations in Theory and Practice*. Dordrecht, Germany: Kluwer Academic Publishers, pp. 323–340.

Price, P.W., Roininen, H. *et al.* (2005) Adaptive radiation into ecological niches with eruptive dynamics: a comparison of tenthredinid and diprionid sawflies. *Journal of Animal Ecology* 74, 397–408.

Price, P.W., Denno, R.F. *et al.* (2011) *Insect Ecology: Behaviour, Populations and Communities*. Cambridge, UK: Cambridge University Press.

Price, T. (1997) Correlated evolution and independent contrasts. *Philosophical Transactions of the Royal Society of London B* 352, 519–529.

Price, T. and Schluter, D. (1991) On the low heritability of life-history traits. *Evolution* 45, 853–861.

Prigogine, I. (1980) *From Being to Becoming: Time and Complexity in the Physical Sciences*. San Francisco, California, USA: W.H. Freeman.

Pritchard, G. (1983) Biology of Tipulidae. *Annual Review of Entomology* 28, 1–22.

Prokopy, R.J. and Owens, E.D. (1983) Visual detection of plants by herbivorous insects. *Annual Review of Entomology* 28, 337–364.

Prospero, J.M. and Lamb, P.J. (2003) African droughts and dust transport to the Caribbean: climate change implications. *Science* 302, 1024–1027.

Proverbs, M.D. (1969) Induced sterilization and control in insects. *Annual Review of Entomology* 14, 82–102.

Prowell, D.P., McMichael, M. *et al.* (2004) Multilocus genetic analysis of host use, introgression, and speciation in host strains of fall armyworm (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America* 97, 1034–1044.

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *The American Naturalist* 132, 652–661.

Punnett, R.C. (1912) *Mendelism*, 3rd edn. London, UK: Macmillan.

Purcell, A.H. and Frazier, N.W. (1985) Habitats and dispersal of the principal leafhopper vectors of

Pierce's disease in the San Joaquin Valley. *Hilgardia* 53, 1–33.

Putnam, R.J. (1977) Dynamics of the blowfly *Calliphora erythrocephala* within carrion. *Journal of Animal Ecology* 46, 853–866.

Putnam, R.J. and Wratten, S.D. (1984) *Principles of Ecology*. London, UK: Croom-Helm.

Puttler, B. (1967) Interrelationship of *Hyperia postica* (Coleoptera: Curculionidae) and *Bathyplectes curculionis* (Hymenoptera: Ichneumonidae) in the eastern United States with particular reference to encapsulation of the parasite eggs by the weevil larvae. *Annals of the Entomological Society of America* 60, 1031–1037.

Qaim, M. and Zilberman, D. (2003) Yield effects of genetically modified crops in developing countries. *Science* 299, 900–902.

Quicke, D.J. (1997) *Parasitic Wasps*. London, UK: Chapman & Hall.

Quinn, H.E., Gatton, M.L. *et al.* (2005) Analysis of Barmah Forest virus disease activity in Queensland, Australia, 1993–2003: identification of a large, isolated outbreak of disease. *Journal of Medical Entomology* 42, 882–890.

Radcliffe, E.B. (1982) Insect pests of potato. *Annual Review of Entomology* 27, 173–204.

Radcliffe, E.B., Hutchison, W.D. *et al.* (2008) *Integrated Pest Management*. Cambridge, UK: Cambridge University Press.

Rader, R., Howlett, B.G. *et al.* (2009) Alternative pollinator taxa are equally efficient but not as effective as the honey bee in a mass flowering crop. *Journal of Applied Ecology* 46, 1080–1087.

Raffa, K.F. and Berryman, A.A. (1987) Interacting selective pressures in conifer-bark beetle systems: a basis for reciprocal adaptations? *The American Naturalist* 129, 234–262.

Raghu, S., Purcell, M.F., *et al.* (2013) Catchment context and the bottom-up regulation of the abundance of specialist semi-aquatic weevils on water hyacinth. *Ecological Entomology* 38, 117–122.

Raguso, R.A. (2009) Floral scent in a whole-plant context: moving beyond pollinator attraction. *Functional Ecology* 23, 837–840.

Rainey, R.C. (1951) Weather and the movement of locust swarms: a new hypothesis. *Nature* 168, 1057–1060.

Rainey, R.C. (1989) *Migration and Meteorology*. Oxford, UK: Clarendon Press.

Rancourt, B., Vincent, C. *et al.* (2000) Circadian activity of *Lygus lineolaris* (Hemiptera: Miridae) and effectiveness of sampling procedures in strawberry fields. *Journal of Economic Entomology* 93, 1160–1166.

Randall, M.G.M. (1982) The dynamics of an insect population throughout its altitudinal distribution: *Coleophora alticolella* (Lepidoptera) in northern England. *Journal of Animal Ecology* 51, 993–1016.

Rankin, M.A. and Burchsted, J.C.A, (1992) The cost of migration in insects. *Annual Review of Entomology* 37, 533–560.

Ranta, E., Kaitala, V. *et al.* (1997a) The Moran effect and synchrony in population dynamics. *Oikos* 78, 136–142.

Ranta, E., Kaitala, V. *et al.* (1997b) The spatial dimension in population fluctuations. *Science* 278, 1621–1623.

Rasmann, S. and Turlings, T.C.J. (2008) First insights into specificity of below-ground tritrophic interactions. *Oikos* 117, 362–369.

Rasmann, S., Kollner, T.G. *et al.* (2005) Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature* 434, 732–737.

Ratcliffe, J.M. and Nydam, M.L. (2008) Multimodal warning signals for a multiple predator world. *Nature* 455, 96–99.

Rathcke, B.J. and Price, P.W. (1976) Anomalous diversity of tropical ichneumonid parasitoids: a predation hypothesis. *The American Naturalist* 110, 889–893.

Raunkaier, C. (1934) *The Life form of Plants and Statistical Plant Geography*. Oxford, UK: Clarendon Press.

Rausher, M.D. (1978) Search image for leaf shape in a butterfly. *Science* 200, Issue 4345, 1071–1073.

Ravenscroft, N.O.M. and Young, M.R. (1996) Habitat specificity, restricted range and metapopulation persistence of the slender Scotch burnet moth *Zygaena loti* in western Scotland. *Journal of Applied Ecology* 33, 993–1000.

Raw, A. (1975) Territoriality and scent marking by *Centris* males (Hymenoptera: Anthophoridae) in Jamaica. *Behaviour* 54, 311–321.

Raw, A. (1984) The nesting biology of nine species of Jamaican bees. *Revista Brasiliera Entomologia* 28, 497–506.

Raw, A. (1985) The ecology of Jamaican bees. *Revista Brasiliera Entomologia* 30, 345–361.

Rayner, J.M.V. (1979) A vortex theory of animal flight. *Journal of Fluid Mechanics* 91, 697–763.

Rea, J.H., Cameron, P.J. *et al.* (2003) Evaluation of insecticides for the control of the green vegetable bug, *Nezara viridula* (L.) (Hemiptera: Pentatomidae), on sweet corn, *Zea mays* (L.), in New Zealand. *International Journal of Pest management* 49, 105–108.

Readshaw, J.I. (1966) The ecology of the swede midge, *Contarinia nasturtii* (Kieff.) (Diptera: Cecidomyiidae). 1. Life history and influence of temperature and moisture on development. *Bulletin of Entomological Research* 56, 685–700.

Real, L. (ed.) (1983) *Pollination Biology*. San Diego, California, USA: Academic Press.

Reavey, C.E., Beare, L. *et al.* (2014) Parental care influences social immunity in burying beetle larvae. *Ecological Entomology* 39, 395–398.

Redak, R.A., Purcell, A.H. *et al.* (2004) The biology of xylem fluid-feeding insect vectors of *Xylella fastidiosa* and their relation to disease epidemiology. *Annual Review of Entomology* 49, 243–270.

Reddy, K.R. and Hodges, H.F. (2000) (eds) *Climate Change and Global Crop Productivity*. Wallingford, UK: CAB International.

Redfern, M. and Cameron, R.A.D. (1978) Population dynamics of the yew gall midge *Taxomyia taxi* (Inchbald) (Diptera: Cecidomyiidae). *Ecological Entomology* 3, 251–263.

Redfern, M. and Hunter, M.D. (2005) Time tells: long-term patterns in the population dynamics of the yew gall midge, *Taxomyia taxi* (Cecidomyiidae). *Ecological Entomology* 30, 86–95.

Reed, D.L., Light, J.E. *et al.* (2007) Pair of lice lost or parasites regained: the evolutionary history of anthropoid primate lice. *BMC Biology* 5, 7.

Reed, S.C., Cleveland, C.C. *et al.* (2011) Functional ecology of free-living nitrogen fixation: a contemporary perspective. *Annual Review of Ecology, Evolution and Systematics* 42, 489–512.

Rees, C.J.C. (1986) Skeletal economy in certain herbivorous beetles as an adaptation to a poor dietary supply of nitrogen. *Ecological Entomology* 11, 221–228.

Rees, D. (2004) *Insects of Stored Products*. London, UK: CSIRO/Manson Publishing.

Rees, N.E. and Onsager, J.A. (1985) Parasitism and survival among rangeland grasshoppers in response to suppression of robber fly (Diptera: Asilidae) predators. *Environmental Entomology* 14, 20–23.

Reeve, J.D. (1997) Predation and bark beetle dynamics. *Oecologia* 112, 48–54.

Reeve, J.D., Rhodes, D.J. *et al.* (1995) Scramble competition in the southern pine beetle, *Dendroctonus frontalis*. *Ecological Entomology* 23, 433–443.

Reeve, J.D., Turchin, P. *et al.* (2002) Evidence for predator-prey cycles in a bark beetle. In: Berryman, A.A. (ed.) *Population Cycles: Evidence for Trophic Interactions*. Oxford, UK: Oxford University Press.

Regal, P.J. (1977) Ecology and evolution of flowering plant dominance. *Science* 196, 622–629.

Regniere, J. and Nealis, V.G. (2008) The fine-scale population dynamics of spruce budworm: survival of early instars related to forest condition. *Ecological Entomology* 33, 362–373.

Reinecke, A., Ruther, J. *et al.* (2006) Optimized trap lure for male *Melolontha* cockchafers. *Journal of Applied Entomology* 130, 171–176.

Reinhard, J., Srinivasan, M.V. *et al.* (2004) Scent-triggered navigation in honey bees. *Nature* 427, 411.

Reinhardt, K. and Siva-Jothy, M.T. (2007) Biology of the bed bugs. *Annual Review of Entomology* 52, 351–374.

Reitz, S.R. and Trumble, J.T. (2002) Competitive displacement among insects and arachnids. *Annual Review of Entomology* 47, 435–465.

Relina, L.I. and Gulevsky, A.K. (2003) A possible role for molecular chaperones in cold adaptation. *Cryo Letters* 24, 203–212.

Remmel, T., Tammaru, T. *et al.* (2009) Seasonal mortality trends in tree-feeding insects: a field experiment. *Ecological Entomology* 34, 98–106.

Renwick, J.A.A. and Chew, F.S. (1994) Oviposition behavior in Lepidoptera. *Annual Review of Entomology* 39, 377–400.

Resh, V.H. and Cardé, R.T. (eds) (2003) *Encyclopaedia of Insects*. New York, New York, USA: Academic/Elsevier Science.

Rettenmeyer, C.W. (1970) Insect mimicry. *Annual Review of Entomology* 15, 43–74.

Reuter, O.M. (1875) Remarques sur le polymorphisme des hémiptères. *Annales de la Societée Entomologique de France*, Serie 5, 5, 225–236.

Reynolds, A.M., Reynolds, D.R. *et al.* (2007) Appetitive flight patterns of male *Agrotis segetum* moths over landscape scales. *Journal of Theoretical Biology* 245, 141–149.

Reynolds, D.R., Chapman, J.W. *et al.* (2005) Radar studies of the vertical distribution of insects migrating over southern Britain: the influence of temperature inversions on nocturnal layer concentrations. *Bulletin of Entomological Research* 95, 257–274.

Reynolds, D.R., Smith, A.D. *et al.* (2008) A radar study of emigratory flight and layer formation by insects at dawn over southern Britain. *Bulletin of Entomological Research* 98, 35–52.

Reynolds, S. (2011) How many insect species? Long live phenodiversity! *Antenna* 35, 87–89.

Reynolds, S. (2012a) The tax that insect pests take from our food. *Antenna* 36, 3–5.

Reynolds, S. (2012b) Economic entomology: how much are insects worth? *Antenna* 36, 83–87.

Rhainds, M., Kettela, E.G. *et al.* (2012) Thirty-five years of pheromone-based mating disruption studies with *Choristoneura fumiferanae* (Clemens) (Lepidoptera: Tortricidae). *The Canadian Entomologist* 144, 380–395.

Rhoades, D.F. (1985) Offensive–defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *The American Naturalist* 125, 205–238.

Rhoades, D.F. and Cates, R.G. (1976) Toward a general theory of plant antiherbivore chemistry. *Recent Advances in Phytochemistry* 10, 168–213.

Ribbands, C.R. (1949) The foraging method of individual honey bees. *Journal of Animal Ecology* 18, 47–66.

Ribeiro, J.M.C. and Francischetti, I.M.B. (2003) Role of arthropod saliva in blood feeding: sialome and post-sialome perspectives. *Annual Review of Entomology* 48, 73–88.

Ribeiro, J.M.C. and Kidwell, M.G. (1994) Transposable elements as population drive mechanisms: specification of critical parameter values. *Journal of Medical Entomology* 31, 10–16.

Ribeiro, L.M.S., Wanderley-Teixeira, V. *et al.* (2014) Fitness costs associated with field-evolved resistance to chlorantraniliprole in *Plutella xylostella* (Lepidoptera: Plutellidae). *Bulletin of Entomological Research* 104, 88–96.

Richards, C.S., Price, B.W. *et al.* (2009) Thermal ecophysiology of seven carrion-feeding blow flies in Southern Africa. *Entomologia Experimentalis et Applicata* 131, 11–19.

Richards, O.W. (1961) The theoretical and practical study of insect populations. *Annual Review of Entomology* 6, 147–162.

Richards, O.W. and Davies, R.G. (1988) *Imms' General Textbook of Entomology*, 10th edn. London, UK: Chapman and Hall.

Richards, O.W. and Waloff, N (1948) The hosts of four British Tachinidae (Diptera). *Entomologist's Monthly Magazine* 84, 127.

Richards, O.W. and Waloff, N (1954) Studies on the biology and population dynamics of British grasshoppers. *Anti-Locust Bulletin* 17, 1–182.

Richards, P.W. (1963) What the tropics can contribute to ecology. *Journal of Ecology* 51, 231–241.

Richards, P.W. (1966) *The Tropical Rain Forest*. Cambridge, UK: Cambridge University Press.

Richardson, M.L., Mitchell, R.F. *et al.* (2010) Causes and consequences of cannibalism in noncarnivorous insects. *Annual Review of Entomology* 55, 39–53.

Ricketts, T.H. (2001) The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* 158, 87–99.

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science* 235, 167–171.

Riddick, E.W. and Barbosa, P. (1998) Impact of Cry3A-intoxicated *Leptinotarsa decemaculata* (Coleoptera: Chrysomelidae) and pollen on consumption, development, and fecundity of *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Annals of the Entomological Society of America* 91, 303–307.

Ridley, M. (1988) Mating frequency and fecundity in insects. *Biological Reviews* 63, 509–549.

Riechert, S.E. and Lockley, T. (1984) Spiders as biological control agents. *Annual Review of Entomology* 29, 299–320.

Rieppel, O. (2004) The language of systematics, and the philosophy of "total evidence". *Systematics and Biodiversity* 2, 9–19.

Ries, L. and Debinski, D.M. (2001) Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. *Journal of Animal Ecology* 70, 840–852.

Riley, J.R., Cheng, X-N. *et al.* (1991) The long-distance migration of *Nilaparvata lugens* (Stål.) (Delphacidae) in China: radar observations of mass return flight in autumn. *Ecological Entomology* 16, 471–489.

Rind, D. (1999) Complexity and climate. *Science* 284, 105–107.

Rind, D. (2002) The Sun's role in climate variation. *Science* 296, 673–677.

Ripper, W.E. (1944) Biological control as a supplement to chemical control of insect pests. *Nature* 153, 448–452.

Risch, S. (1981) Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. *Ecology* 62, 1325–1340.

Robert, V., Macintyre, J., *et al.* (2003) Malaria transmission in urban, sub-Saharan Africa. *American Journal of Tropical Medicine and Hygiene* 68, 169–176.

Roberts, S.P., Harrison, J.F. *et al.* (1998) Mechanisms of thermal heat balance in flying *Centris pallida* (Hymenoptera; Anthophoridae). *Journal of Experimental Biology* 201, 2321–2331.

Robertson, H.M. (1985) Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: females mimicking males. *Animal behaviour* 33, 805–809.

Robinson, G.E. (2004) Beyond nature and nurture. *Science* 304, 397–399.

Robinson, G.S. (1975) *Macrolepidoptera of Fiji and Rotuma*. London, UK: E.W. Classey.

Robinson, T. (1974) Metabolism and function of alkaloids in plants. *Science* 184, 430–435.

Rochat, J. and Gutierrez, A.P. (2001) Weather-mediated regulation of olive scale by two parasitoids. *Journal of Animal Ecology* 70, 476–490.

Rockwood, L.L. (2006) *An Introduction to Population Ecology*. Oxford, UK: Blackwell.

Rodriguez, W.C. and Bass, W.M. (1983) Insect activity and its relationship to decay rates of human cadavers in East Tennessee. *Journal of Forensic Sciences* 28, 423–432.

Roff, D.A. (1977) Dispersal in dipterans: its costs and consequences. *Journal of Animal Ecology* 46, 443–456.

Roff, D.A. (1984) The cost of being able to fly: A study of wing polymorphism in two species of crickets. *Oecologia* 63, 30–37.

Roff, D.A. (1986) The evolution of wing polymorphism in insects. *Evolution* 40, 1009–1020.

Roff, D.A. (1990) The evolution of flightlessness in insects. *Ecological Monographs* 60, 389–421.

Roff, D.A. (1994) Habitat persistence and the evolution of wing dimorphism in insects. *The American Naturalist* 144, 733–798.

Roff, D.A. (2002) *Life History Evolution*. Sunderland, Massachusetts, USA: Sinauer Associates.

Roff, D.A. and Emerson, K. (2006) Epistasis and dominance: evidence for differential effects in life-history versus morphological traits. *Evolution* 60, 1981–1990.

Rogers, A.R. (1990) Group selection by selective emigration: the effects of migration and kin structure. *The American Naturalist* 135, 398–413.

Rogers, D.J. and Randolph, S.E. (1985) Population ecology of tsetse. *Annual Review of Entomology* 30, 197–216.

Rogers, D.J. and Williams, B.G. (1994) Tsetse distribution in Africa: seeing the wood and the trees. In: Edwards, P.J., May, R.M. *et al.* (eds) *Large-scale Ecology and Conservation Biology*. Oxford, UK: Blackwell Scientific, pp. 247–272.

Rogers, D. J., Ward, A.L. *et al.* (2005) Damage potential of two scarab species on groundnuts. *International Journal of Pest Management* 51, 307–314.

Rogers, M.E., Chance, M.L. *et al.* (2002) The role of promastigote secretory gel in the origin and transmission of the infective stage of *Leishmania mexicana* by the sandfly *Lutzomyia longipalpis*. *Parasitology* 124, 495–507.

Rohani, P., Lewis, T.J. *et al.* (1997) Spatial self-organisation in ecology: pretty patterns or robust reality? *Trends in Ecology and Evolution* 12, 70–74.

Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65, 514–527.

Roitberg, B.D., Sircom, J. *et al.* (1993) Life expectancy and reproduction. *Nature* 364, 108.

Roitberg, B.D., Mondor, E.B. *et al.* (2003) Pouncing spider, flying mosquito: blood acquisition increases predation risk in mosquitoes. *Behavioral Ecology* 14, 736–740.

Roland, J. (1994) After the decline: what maintains low winter moth density after successful biological control? *Journal of Animal Ecology* 63, 392–398.

Roland, J. (1998) The population dynamics of *Operophtera brumata* (Lepidoptera: Geometridae). In: Dempster, J.P. and McLean, I.G.F. (eds) *Insect Populations in Theory and in Practice*, Dordrecht, Germany: Kluwer, pp. 309–321.

Roland, J. and Embree, D.G. (1995) Biological control of the winter moth. *Annual Review of Entomology* 40, 475–492.

Roland, J. and Myers, J.H. (1987) Improved insect performance from host-plant defoliation: winter moths on oak and apple. *Ecological Entomology* 12, 409–414.

Roland, J. and Taylor, P.D. (1997) Insect parasitoid species respond to forest structure at different spatial scales. *Nature* 386, 710–713.

Roland, J., Denford, K.E. *et al.* (1995) Borneol as an attractant for *Cyzenis albicans*, a tachinid parasitoid of the winter moth, *Operophtera brumata* L. (Lepidoptera: Geometridae). *The Canadian Entomologist* 127, 413–221.

Romeis, J., Babendreier, D. *et al.* (2003) Consumption of snowdrop lectin (*Galanthus nivalis* agglutinin) causes direct effects on adult parasitic wasps. *Oecologia* 134, 528–536.

Room, P.M., Julien, M.H. *et al.* (1989) Vigorous plants suffer most from herbivores: latitude, nitrogen and biological control of the weed *Salvinia molesta*. *Oikos* 54, 92–100.

Root, R.B. (1967) The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* 37, 317–350.

Root, R.B. (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleracea). *Ecological Monographs* 43, 95–124.

Root, R.B. and Kareiva, P.M. (1984) The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequences and adaptive significance of Markovian movements in a patchy environment. *Ecology* 65, 147–165.

Rose, D.J.W., Page, W.W. *et al.* (1985) Downwind migration of the African armyworm moth, *Spodoptera exempta*, studied by mark-and-capture and by radar. *Ecological Entomology* 10, 299–313.

Rosenberg, L.J. and Magor, J.I. (1983) Flight duration of the brown planthopper. *Nilaparvata lugens* (Homoptera: Delphacidae). *Ecological Entomology* 8, 341–350.

Rosenheim, J.A. (1987) Host location and exploitation by the cleptoparasitic wasp *Argochrysis chk armilla*: the role of learning (Hymenoptera: Chrysididae). *Behavioral Ecology and Sociobiology* 21, 401–406.

Rosenheim, J.A. (1998) Higher-order predators and the regulation of insect herbivore populations. *Annual Review of Entomology* 43, 421–447.

Rosenheim, J.A. (1999a) Characterising the cost of oviposition in insects: a dynamic model. *Evolutionary Ecology* 13, 141–165.

Rosenheim, J.A. (1999b) The relative contributions of time and eggs to the cost of reproduction. *Evolution* 53, 376–385.

Rosenheim, J.A., Jepsen, S.J. *et al.* (2008) Time limitation, egg limitation, the cost of oviposition, and lifetime reproduction by an insect in nature. *The American Naturalist* 172, 486–496.

Rosenthal, G.A. (1986) The chemical defenses of higher plants. *Scientific American* 254, 76–81.

Rosenzweig, M.L. and MacArthur, R.H. (1963) Graphical representation and stability conditions of predator-prey interaction. *The American Naturalist* 97, 209–223.

Ross, D.W. and Wallin, K.F. (2008) High release rate 3-methylcyclohex-2-en-1-one dispensers prevent Douglas-fir beetle (Coleoptera: Curculionidae) infestation of live Douglas fir. *Journal of Economic Entomology* 101, 1826–1830.

Ross, H.H. (1958) Further comments on niches and natural co-existence. *Evolution* 12, 112–113.

Ross, R. (1911) *The Prevention of Malaria*, 2nd edn. London, UK: John Murray.

Rossi, M.N. and Fowler, H.G. (2003) The sugarcane borer, *Diatraea saccharalis*, (Fabr.) (Lep,. Crambidae) and its parasitoids: a synchrony approach to spatial and temporal dynamics. *Journal of Applied Entomology* 127, 200–208.

Rossiter, M.C. (1991) Environmentally-based maternal effects: a hidden force in insect population dynamics. *Oecologia* 87, 288–294.

Rossiter, M.C. (1996) Incidence and consequences of inherited environmental effects. *Annual Review of Ecology and Systematics* 27, 451–476.

Rotheray, G.E. (1984) Host relations, life cycles and multiparasitism in some parasitoids of aphidophagous Syrphidae. *Ecological Entomology* 9, 303–310.

Rothery, P. (1998) The problems associated with the identification of density dependence in population data. In: Dempster, J.P. and McLean, I.G.F. (eds) *Insect Populations in Theory and in Practice*. Dordrecht, Germany: Kluwer, pp. 97–133.

Rothschild, E.G. (2001) *Economic sentiments: Adam Smith, Condorcet, and the Enlightenment*. Cambridge, Massachusetts, USA: Harvard University Press.

Rothschild, M. (1972) Secondary plant substances and warning colouration in insects. Symposia of the Royal Entomological Society of London 6, 59–83.

Rothschild, M. (1984) Aide mémoire mimicry. *Ecological Entomology* 9, 311–319.

Rothschild, M. and Clay, T. (1952) *Fleas, Flukes and Cuckoos*. London, UK: Collins.

Rothschild, N.C. (1903) New species of Siphonaptera from Egypt and the Sudan. *Entomologist's Monthly Magazine* 39, 83–87.

Roush, R.T. and Tabashnik, B.E. (1990) *Pesticide Resistance in Arthropods*. New York, New York, USA: Chapman and Hall.

Rowland, H. M. (2009) From Abbott Thayer to the present day: what have we learned about the function of countershading? *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 364(1516), 519–527. doi:10.1098/rstb.2008.0261.

Rowland, H.M., Cuthill, I.C. *et al.* (2008) Can't tell the caterpillars from the trees: Countershading enhances survival in a woodland. *Proceedings of the Royal Society B* 275, 2539–2545.

Royama, T. (1977) Population persistence and density dependence. *Ecological Monographs* 47, 1–35.

Royama, T. (1981) Evaluation of mortality factors in insect life table analysis. *Ecological Monographs* 51, 495–505.

Royama, T. (1984) Population dynamics of the spruce budworm, *Choristoneura fumiferana*. *Ecological Monographs* 54, 429–462.

Royama, T. (1992) *Analytical Population Dynamics*. London, UK: Chapman and Hall.

Royama, T. (1996) A fundamental problem in key factor analysis. *Ecology* 77, 87–93.

Royama, T. (2001) Measurement, analysis, and interpretation of mortality factors in insect survivorship studies, with reference to the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *Population Ecology* 43, 157–178.

Ruberson, J.R. (ed.) (1999) *Handbook of Pest Management*. New York, New York, USA: Marcel Dekker.

Rubio, A., Bellocq, M.I. *et al.* (2013) Macro- and micro-environmental factors affecting tyre-breeding flies (Insecta: Diptera) in urbanised areas. *Ecological Entomology* 38, 303–314.

Rudinsky, J.A. (1962) Ecology of Scolytidae. *Annual Review of Entomology* 7, 327–348.

Ruiu, L., Delrio, G. *et al.* (2005) Lethal and sublethal effects of *Brevibacillus laterosporus* on the house fly (*Musca domestica*). *Entomologia Experimentalis et Applicata* 118, 137–144.

Rull, J., Aluja, M. *et al.* (2011) Distribution and basic biology of black cherry-infesting *Rhagoletis* (Diptera: Tephritidae) in Mexico. *Annals of the Entomological Society of America* 104, 202–211.

Russell, B. (1961) *History of Western Philosophy*, 2nd edn. London, UK: Allen and Unwin. Reprinted 2004, Routledge Classics.

Russell, R.C. (2002) Ross River virus: ecology and distribution. *Annual Review of Entomology* 47, 1–31.

Ruxton, G.D. (1996) Dispersal and chaos in spatially structured models: an individual-level approach. *Journal of Animal Ecology* 65, 161–169.

Ruxton, G., Gonzalez-Andujar, J.L. *et al.* (1997) Mortality during dispersal stabilises local population fluctuations. *Journal of Animal Ecology* 66, 289–292.

Ryan, K., Moncalvo, J-M. *et al.* (2011) Interactions between the fungal symbiont of *Sirex noctilio* (Hymenoptera: Siricidae) and two bark beetle-vectored fungi. *The Canadian Entomologist* 143, 224–235.

Saccheri, I.J. *et al.* (1998) Inbreeding and extinction in a butterfly metapopulation. *Nature* 392, 491–494.

Safranyik, L., Carroll, A.L. *et al.* (2010) Potential for range expansion of mountain pine beetle into the boreal forest of North America. *The Canadian Entomologist* 142, 415–442.

Saikkonen, K., Faeth, S.H. *et al.* (1998) Fungal endophytes: a continuum of interactions with host plants. *Annual Review of Ecology and Systematics* 29, 319–343.

Sallam, N. (2011) Review of current knowledge on the population dynamics of *Dermolepida albohirtum* (Coleoptera: Scarabaeidae). *Australian Journal of Entomology* 50, 300–308.

Salt, G. (1935) Experimental studies in insect parasitism 3. – host selection. *Proceedings of the Royal Society B* 117, 413–435.

Salt, G. (1952) Trimorphism in the ichneumonid parasite Gelis corruptor. *Quarterly Journal of Microscopical Science* 93, 453–474.

Salt, G. (1968) The resistance of insect parasitoids to the defence reactions of their hosts. *Biological Reviews* 43, 200–232.

Salt, R.W. (1961) Principles of insect cold-hardiness. *Annual Review of Entomology* 6, 55–74.

Salvo, A. and Valladares, G.R. (1997) An analysis of leaf-miner and plant host ranges of three *Chrysocharis* species (Hym.: Eulophidae) from Argentina. *Entomophaga* 42, 417–426.

Sampson, B.J., Stringer, S.J. *et al.* (2002) *Dasineura oxycoccana* (Diptera: Cecidomyiidae) in blueberry. *Environmental Entomology* 31, 339–347.

Sanders, C.J., Stark, R.W. *et al.* (1985) (eds) *Recent Advances in Spruce Budworm Research*. Ottawa, Canada: Canadian Forest Service.

Sandler, L. and Novitski, E. (1957) Meiotic drive as an evolutionary force. *The American Naturalist* 91, 105–110.

Sandvik, G., Seip, K.L. *et al.* (2002) An anatomy of interactions driving species in a seasonal world. *Oikos* 99, 260–271.

Sane, S.P., Dieudonné, A. *et al.* (2007) Antennal mechanosensors mediate flight control in moths. *Science* 315, 863–866.

Sapp, J. (1994) *Evolution by Association: A History of Symbiosis*. Oxford, UK: Oxford University Press.

Sappington, T.W. and Showers, W.B. (1992) Reproductive maturity, mating status, and long-duration flight behavior of *Agrostis ipsilon* (Lepidoptera: Noctuidae) and the conceptual misuse of the oogenesis-flight syndrome by entomologists. *Environmental Entomology* 21, 677–688.

Sappington, T.W., Arnold, M.D. *et al.* (2006) Dispersal of boll weevils (Coleoptera: Curculionidae) from cotton modules before ginning. *Journal of Economic Entomology* 99, 67–75.

Sargent, T.D. (1990) Startle as an anti-predator mechanism, with special reference to the underwing moths, (*Catocala*). In: Evans, D.L. and Schmidt, J.U. (eds) *Insect Defences: Adaptive Mechanisms and Strategies of Prey and Predators*. Albany, New York, USA: State University of New York, pp. 229–249.

Sarvary, M.A., Hajek, A.E. *et al.* (2016) Investigating the effects of symbiotic fungi on the flight behaviour of *Sirex noctilio* (Hymenoptera: Siricidae). *The Canadian Journal of Entomology* 148, 543–541.

Sattler, K. (1991) A review of wing reduction in Lepidoptera. *Bulletin of the British Museum* 60, 243–288.

Savage, V.M., Gillooly, J.F. *et al.* (2004) The predominance of quarter-power scaling in biology. *Functional Ecology* 18, 257–282.

Schaefer, C.W. and Panizzi, A.R. (2000) *Heteroptera of Economic Importance*. New York, New York, USA: CRC Press.

Schaefer, H.M. and Ruxton, G.D. (2009) Deception in plants: mimicry or perceptual exploitation. *Trends in Ecology and Evolution* 24, 676–685.

Schaffer, W.M. (1985) Order and chaos in ecological systems. *Ecology* 66, 93–106.

Schauff, M.E., LaSalle, J. *et al.* (1998) The genera of chalcid parasitoids (Hymenoptera: Chalcidoidea) of citrus leafminer *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae). *Journal of Natural History* 32, 1001–1056.

Scheerer, M. (1963) Problem solving. *Scientific American* 208, 118–128.

Schemske, D.W., Mittelbach, G.G. *et al.* (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution and Systematics* 40, 245–269.

Schenk, D., Bersier, L-F. *et al.* (2005) An experimental test of the nature of predation: neither prey- nor ratio-dependent. *Journal of Animal Ecology* 74, 86–91.

Schiffer, M., Kennington, W.J. *et al.* (2007) Lack of genetic structure among ecologically adapted populations of an Australian rainforest *Drosophila* species as indicated by microsatellite markers and DNA sequences. *Molecular Ecology* 16, 1687–1700.

Schluter, D. (2001) Ecology and the origin of species. *Trends in Ecology and Evolution* 16, 372–380.

Schmid-Hempel, P. (1998) *Parasites in Social Insects*. Princeton, New Jersey, USA: Princeton University Press.

Schmid-Hempel, P. (2005) Evolutionary ecology of insect immune defenses. *Annual Review of Entomology* 50, 529–551.

Schmid-Hempel, P. and Schmid-Hempel, R. (1988) Parasitic flies (Conopidae, Diptera) may be important stress factors for the ergonomics of their bumblebee hosts. *Ecological Entomology* 13, 469–472.

Schmieder, R.G. (1933) The polymorphic forms of *Melittobia chalybii* Ashmead and the determining factors involved in their production. *Biological Bulletin* 65, 338–354.

Schneider, F. (1969) Bionomics and Physiology of aphidophagous Syrphidae. *Annual Review of Entomology* 14, 103–124.

Schoener, T.W. (1984) Counters to the claims of Walter *et al.* on the evolutionary significance of competition. *Oikos* 43, 248–250.

Schoenly, K. (1990) The predators of insects. *Ecological Entomology* 15, 333–345.

Schofield, C.J. (1979) The behaviour of Triatominae. *Bulletin of Entomological Research* 69, 363–379.

Scholl, P.J. (1993) Biology and control of cattle grubs. *Annual Review of Entomology* 39, 53–70.

Schroder, R., Cristescu, S.M. *et al.* (2007) Reduction of ethylene emission from Scots pine elicited by egg secretion. *The Journal of Experimental Botany* 58, 1835–1842.

Schrödinger, E. (1944) *What is Life*? Cambridge, UK: Cambridge University Press.

Schroeder, L.M. (1996) Interactions between the predators *Thanasimus formicarius* (Col: Cleridae) and *Rhizophagus depressus* (Col: Rhizophagidae), and the bark beetle *Tomicus piniperda* (Col: Scolytidae). *Entomophaga* 41, 63–75.

Schtickzelle, N. and Baguette, M. (2003) Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. *Journal of Animal Ecology* 72, 533–545.

Schuett, W., Dall, S.R.X. *et al.* (2015) Life-history tradeoffs mediate "personality" variation in two colour morphs of the pea aphid, *Acyrthosiphon pisum*. *Journal of Animal Ecology* 84, 90–101.

Schuh, R.T. and Slater, J.A. (1995) *True Bugs of the World* (*Hemiptera: Heteroptera*). Ithaca, New York, USA: Cornell University Press.

Schultz, F., Francke, W. *et al.* (1990) Male pheromone of swift moth, *Hepialus hecta*, L. (Lepidoptera: Hepialidae). *Journal of Chemical Ecology* 16, 3511–3521.

Schultz, J.C. (1988) Many factors influence the evolution of herbivore diets, but plant chemistry is central. *Ecology* 69, 896–897.

Schultz, M.G. and Morens, D.M. (2009) Charles-Jules-Henri Nicolle. *Emerging Infectious Diseases* 15, 1520–1522.

Schwerdtfeger, F. (1935) *Studien über den Massenwechsel einiger Forstschädlinge*. Berlin: Springer.

Schwerdtfeger, F. (1941) Über die Ursachen des Massenwechsels der Insekten. *Zeitschrift für angewandte Entomologie* 28, 254–303.

Scott, A.C., Stephenson, J. *et al.* (1992) Interaction and coevolution of plants and arthropods during the Palaeozoic and Mesozoic. *Philosophical Transactions of the Royal Society B* 335, 129–165.

Scott, K.D., Wilkinson, K.S. *et al.* (2005) Gene-flow between populations of cotton bollworms *Helicoverpa armigera* Hubner (Lepidoptera: Noctuidae) is highly variable between years. *Bulletin of Entomological Research* 95, 381–392.

Scott, M.P. (1998) The ecology and behavior of burying beetles. *Annual Review of Entomology* 43, 595–618.

Seastedt, T.R., Ramundo, R.A. *et al.* (1988) Maximisation of densities of soil animals by foliage herbivory: empirical evidence, graphical and conceptual models. *Oikos* 51, 243–248.

Sedaghat, M.M., Linton, M.-Y. *et al.* (2003) The *Anopheles maculipennis* complex in Iran: molecular characterisation and recognition of a new species. *Bulletin of Entomological Research* 93, 527–535.

Séguy, E. (1923) *Faune de France 6. Diptères Anthomyides*. Paris, France: Lechevalier.

Seidelmann, K. (2014) Optimal progeny body size in a solitary bee, *Osmia bicornis* (Apoidea: Megachilidae). *Ecological Entomology* 39, 656–663.

Seino, Y., Suzuki, Y. *et al.* (1996) An ovicidal substance produced by rice plants in response to oviposition by the white-backed plant hopper, *Sogatella furcifera* (Horváth) (Homoptera: Delphacidae). *Applied Entomology and Zoology* 31, 467–473.

Servedio, M.R. and Noor, M.A.F. (2003) The role of reinforcement in speciation: theory and data. *Annual Review of Ecology, Evolution and Systematics* 34, 339–364.

Service, M.W. (2000) *Medical Entomology for Students*, 2nd edn. Cambridge, UK: Cambridge University Press.

Sétamou, M., Bernal, J.S. *et al.* (2002) Parasitism and location of sugarcane borer (Lepidoptera: Pyralidae) by *Cotesia flavipes* (Hymenoptera: Braconidae) on transgenic and conventional sugarcane. *Environmental Entomology* 31, 1219–1225.

Settle, W.H., Ariawan, H. *et al.* (1996) Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology* 77, 1975–1988.

Shannag, H.K. and Obeidat, W.M. (2008) Interaction between plant resistance and predation of *Aphis fabae* (Homoptera: Aphididae) by *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Annals of Applied Biology* 152, 331–337.

Shapiro, A.M. (1970) The role of sexual behavior in density-related dispersal in pierid butterflies. *The American Naturalist* 104, 367–372.

Shapiro, A.M. (1981) The pierid red-egg syndrome. *The American Naturalist* 117, 276–294.

Sharov, A.A., Liebhold, A.M. *et al.* (1996) Spatial variation among counts of gypsy moths (Lepidoptera: Lymantriidae) in pheromone-baited traps at expanding population fronts. *Environmental Entomology* 25, 1312–1320.

Shaw, A.K. and Kokko, H. (2014) Mate finding, Allee effects and selection for sex-biased dispersal. *Journal of Animal Ecology* 83, 1256–1267.

Shaw, M.R. (1994) Parasitoid host ranges. In: Hawkins, B.A. and Sheehan, W. (eds) *Parasitoid Community Ecology*. Oxford, UK: Oxford University Press, pp. 111–144.

Shelford, V.E. (1913) The life history of the bee fly, (*Spogostylum anale* Say), etc. *Annals of the Entomological Society of America* 6, 213–225.

Shelton, A.M. and Badenes-Perez, F.R. (2006) Concepts and applications of trap cropping in pest management. *Annual Review of Entomology* 51, 285–308.

Shelton, A.M. and North, R.C. (1986) Species composition and phenology of Thysanoptera within field crops adjacent to cabbage fields. *Environmental Entomology* 15, 513–519.

Sheehan, W. and Hawkins, B.A. (1991) Attack strategy as an indicator of host range in metopiine and pimpline Ichneumonidae (Hymenoptera). *Ecological Entomology* 16, 129–131.

Sheppard, P.M. (1951) A quantitative study of two populations of the moth *Panaxia dominula*. *Heredity* 5, 349–378.

Sheppard, P.M. (1956) Ecology and its bearing on population genetics. *Proceedings of the Royal Society B* 145, 308–315.

Sheppard, P.M. (1975) *Natural Selection and Heredity*, 4th edn. London, UK: Hutchinson.

Sheppard, P.M., MacDonald, W.W. *et al.* (1969) The dynamics of an adult population of *Aedes aegypti* in relation to dengue haemorrhagic fever in Bangkok. *Journal of Animal Ecology* 38, 661–702.

Sherman, G. and Visscher, P.K. (2002) Honey bee colonies achieve fitness through dancing. *Nature* 419, 920–922.

Shindell, D., Rind, D. *et al.* (1999) Solar cycle variability, ozone, and climate. *Science* 284, 305–308.

Shipp, J.L., Buitenhuis, R. *et al.* (2008) Vectoring of Pepino mosaic virus by bumble bees in tomato greenhouses. *Annals of Applied Biology* 153, 149–155.

Shoda-Kagaya, E. (2007) Genetic differentiation of the pine wilt disease vector *Monochamus alternatus* (Coleoptera: Cerambycidae) over a mountain range – revealed from microsatellite DNA markers. *Bulletin of Entomological Research* 97, 167–174.

Shorey, H.H. (1963) The biology of *Trichoplusia ni* (Lepidoptera: Noctuidae) 2. Factors affecting adult fecundity and longevity. *Annals of the Entomological Society of America* 56, 476–480.

Shorey, H.H., Andres, L.A. *et al.* (1962) The biology of *Trichoplusia ni* (Lepidoptera: Noctuidae) 1. Life history and behavior. *Annals of the Entomological Society of America* 55, 591–597.

Shorrocks, B. (1977) An ecological classification of European *Drosophila* species. *Oecologia* 26, 335–345.

Shorrocks, B. (1990) Coexistence in a patchy environment. In: Shorrocks, B. and Swingland, I.R. (eds) *Living in a Patchy Environment*. Oxford, UK: Oxford University Press, pp. 91–106.

Shorrocks, B., Rosewell, J. *et al.* (1984) Interspecific competition is not a major force in many insect communities. *Nature* 310, 310–312.

Showler, A.T. (1995) Locust (Orthoptera: Acrididae) outbreaks in Africa and Asia, 1992–1994: an overview. *American Entomologist* 41, 179–185.

Showler, A.T. (2002) Effects of kaolin-based particle film application on boll weevil (Coleoptera: Curculionidae) injury to cotton. *Journal of Economic Entomology* 95, 754–762.

Shreeve, T.G. (1986) Egg laying by the speckled wood butterfly (*Pararge aegeria*): the role of female behaviour, host plant abundance and temperature. *Ecological Entomology* 11, 229–236.

Sibly, R.M. and Smith, R.H. (1998) Identifying key factors using lambda contribution analysis. *Journal of Animal Ecology* 67, 17–24.

Siebert, M.W., Nolting, S. *et al.* (2008) Efficacy of transgenic cotton expressing Cry1Ac and Cry1F insecticidal proteins against heliothines (Lepidoptera: Noctuidae). *Journal of Economic Entomology* 101, 1950–1959.

Sigsgaard, L. (2002) A survey of aphids and aphid parasitoids in cereal fields in Denmark, and the parasitoid's role in biological control. *Journal of Applied Entomology* 126, 101–107.

Sigsgaard, L. (2007) Early season natural control of the brown planthopper, *Nilaparvata lugens*: the contribution and interaction of two spider species and a predatory bug. *Bulletin of Entomological Research* 97, 533–544.

Siitonen, J. (2001) Forest management, coarse woody debris and saproxylic organisms. *Ecological Bulletin* 49, 11–42.

Sileshi, G. (2006) Selecting the right statistical model for the analysis of insect count data by using information theoretic measures. *Bulletin of Entomological Research* 96, 479–488.

Sillén-Tullberg, B. (1988) Evolution of gregariousness in aposematic butterfly larvae: a phylogenetic analysis. *Evolution* 42, 293–305.

Silva-Torres, C.S.A. and Matthews, R.W. (2003) Development of *Melittobia australica* Girault and *M. digitata* Dahms (Hymenoptera: Eulophidae) parasitising *Neobellieria bullata* (Parker) (Diptera: Sarcophagidae) puparia. *Neotropical Entomology* 32, 645–651.

Simberloff, D. (1981) Competition theory, hypothesis testing, and other community ecological buzzwords. *The American Naturalist* 122, 626–635.

Simberloff, D. and Stiling, P. (1996) How risky is biological control? *Ecology* 77, 1965–1974.

Simberloff, D., Farr, J.A. *et al.* (1992) Movement corridors: conservation bargains or poor investments? *Conservation Biology* 6, 493–504.

Sime, K. (2002) Chemical defence of *Battus philenor* larvae against attack by the parasitoid *Trogus pennator*. *Ecological Entomology* 27, 337–345.

Sime, K.R. and Brower, A.V.Z. (1998) Explaining the latitudinal gradient anomaly in ichneumonid species richness: evidence from butterflies. *Journal of Animal Ecology* 67, 387–399.

Simmonds, F.J. (1948) Some difficulties in determining by means of field samples the true value of parasitic control. *Bulletin of Entomological Research* 39, 435–440.

Simmons, A.D. and Thomas, C.D. (2004) Changes in dispersal during species' range expansion. *The American Naturalist* 164, 378–395.

Simms, E.L. and Rausher, M.D. (1987) Costs and benefits of plant resistance to herbivory. *The American Naturalist* 130, 570–581.

Simms, E.L. and Triplett, J. (1994) Costs and benefits of plant responses to disease: resistance and tolerance. *Evolution* 48, 1973–1985.

Simpson, G.G. (1961) *Principles of Animal Taxonomy*. New York, New York, USA: Columbia University Press.

Sims, S.R. and Shapiro, A.M. (1983) Pupal colour dimorphism in Californian *Battus philenor*: pupation sites, environmental control, and diapause linkage. *Ecological Entomology* 8, 95–104.

Singer, M.S. and Bernays, E.A. (2003) Understanding omnivory needs a behavioral perspective. *Ecology* 84, 2532–2537.

Singer, M.S. and Stireman, J.O. (2003) Does antiparasite defence explain host plant selection by a polyphagous caterpillar? *Oikos* 100, 554–562.

Singh, B., Battu, G.S. *et al.* (1975) Studies on the spider predators of the maize borer, *Chilo partellus* (Swinhoe) in the Punjab. *Indian Journal of Entomology* 37, 72–76.

Singh, B., Kim Sung, L. *et al.* (2004) A large focus of naturally acquired Plasmodium knowlesi infections in human beings. *The Lancet* 363, 1017–1024.

Sinkins, S.P. and Godfray, H.C.J. (2004) Use of *Wolbachia* to drive nuclear transgenes through insect populations. *Proceedings of the Royal Society B* 271, 1421–1426.

Sisojevic, P. (1975) Population dynamics of tachinid parasites of the gypsy moth (*Lymantria dispar* L.) during a gradation period. *Zasitia Bilja* 26, 97–170.

Sisterson, M.S., Biggs, R.W. *et al.* (2007) Effects of *Bt* cotton on insecticide use and abundance of two generalist predators. *Entomologia Experimentalis et Applicata* 124, 305–311.

Sisterson, M.S., Yacoub, R. *et al.* (2008) Distribution and management of citrus in California: implications for management of glassy-winged sharpshooter. *Journal of Economic Entomology* 101, 1041–1050.

Sites, J.W. and Marshall, J.C. (2003) Delimiting species: a renaissance issue in systematic biology. *Trends in Ecology and Evolution* 18, 462–470.

Sivanpillai, R. and Latchininsky, A.V. (2008) Can late summer Landsat data be used for locating Asian migratory locust, *Locusta migratoria migratoria*, oviposition sites in the Amudarya River delta, Uzbekistan? *Entomologia Experimentalis et Applicata* 128, 346–353.

Sivapragasam, A., Ito, Y. *et al.* (1988) Population fluctuations of the diamond-back moth, *Plutella xylostella* (L.), on cabbages in *Bacillus thuringiensis* sprayed and non-sprayed plots, and factors affecting within-generation survival of immatures. *Researches on Population Ecology* 30, 329–341.

Sivinski, J. and Aluja, M. (2003) The evolution of ovipositor length in the parasitic Hymenoptera and the search for predictability in biological control. *Florida Entomologist* 86, 143–150.

Skaf, R., Popov, G.B. *et al.* (1990) The desert locust: an international challenge. *Philosophical Transactions of the Royal Society of London B* 328, 525–538.

Skarpaas, O. and Økland, B. (2009) Timber import and the risk of forest pest introductions. *Journal of Applied Ecology* 46, 55–63.

Skellam, J.G. (1951) Random dispersal in theoretical populations. *Biometrika* 38, 196–218.

Skovgård, H. and Nachman, G. (2004) Biological control of house flies *Musca domestica* and stable flies *Stomoxys calcitrans* (Diptera: Muscidae) by means of inundative releases of *Spalangi cameroni* (Hymenoptera: Pteromalidae). *Bulletin of Entomological Research* 94, 555–567.

Slansky, F. and Feeny, P. (1977) Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated plants. *Ecological Monographs* 47, 209–228.

Slansky, F. and Rodriguez, J.G. (1987) Nutritional ecology of insects, mites, spiders, and related invertebrates: an overview. In: Slansky, F. and Rodriguez, J.G. *Nutritional Ecology of Insects*, *Mites, Spiders*, *and Related Invertebrates*. New York, New York, USA: Wiley.

Slatkin, M. (1974) Competition and regional coexistence. *Ecology* 55, 128–134.

Slatkin, M. (1980) Ecological character displacement. *Ecology* 61, 163–177.

Slatkin, M. (1984) Ecological causes of sexual dimorphism. *Evolution* 38, 622–630.

Slatkin, M. (1985) Gene flow in natural populations. *Annual Review of Ecology and Systematics* 16, 393–430.

Slatkin, M. (1987) Gene flow and the geographic structure of natural populations. *Science* 236, 787–792.

Slobodkin, L.B. (1986) The role of minimalism in art and science. *The American Naturalist* 127, 257–265.

Sloggett, J.J and Honěk, A. (2012) Genetic studies. In: Hodek, I., van Emden, H.F. *et al*. (eds) *Ecology and Behaviour of the Ladybird Beetles*. Oxford, UK: Blackwell, pp. 13–53.

Sloggett, J.J. and Weisser, W.W. (2002) Parasitoids induce the production of the dispersal morph of the pea aphid, *Acyrthosiphon pisum*. *Oikos* 98, 323–333.

Smit, F.G.A.M. (1973) In: Smith, K.G.V. (ed.) *Insects and other Arthropods of Medical Importance*. Publication no. 720. London, UK: British Museum (Natural History).

Smith, A. (1979) Life strategy and mortality factors of *Sceliphron laetum* (Smith) (Hymenoptera: Sphecidae) in Australia. *Australian Journal of Ecology* 4, 181–186.

Smith, A.P. (1973) Stratification of temperate and tropical forests. *The American Naturalist* 107, 671–683.

Smith, B.C. (1960) Note on parasitism of two coccinellids, *Coccinella trifasciata perplexa* Muls. and *Coleomegilla maculata lengi* Timb. (Coleoptera: Coccinellidae) in Ontario. *The Canadian Entomologist* 92, 652.

Smith, C.C. and Fretwell, S.D. (1974) The optimal balance between size and number of offspring. *The American Naturalist* 108, 499–506.

Smith, D.C. (1987) *The Population Dynamics in Jamaica of* Liriomyza commelinae *(Frost) (Diptera, Agromyzidae)*. PhD. thesis, University of the West Indies.

Smith, D.C. (1988) Heritable divergence of *Rhagoletis pomonella* host races by seasonal asynchrony. *Nature* 336, 66–67.

Smith, D.C. and Douglas, A.E. (1987) *The Biology of Symbiosis*. London, UK: Arnold.

Smith, D.R. (2003) Expanding ranges for four species of invasive sawflies (Hymenoptera: Tenthredinidae) in Eastern United States. *Proceedings of the Entomological Society of Washington* 105, 246–248.

Smith, F.E. (1954) Quantitative aspects of population growth. In: Boell, E. (ed.) *Dynamics of Growth Processes*. Princeton, New Jersey, USA: Princeton University Press, pp. 274–294.

Smith, H.S. (1935) The role of biotic factors in the determination of population density. *Journal of Economic Entomology* 28, 873–898.

Smith, J.M. (1957) Effects of the food plant of California red scale, *Aonidiella aurantii* (Mask.) on reproduction of its hymenopterous parasites. *The Canadian Entomologist* 89, 219–230.

Smith, J.W. (1998) Boll weevil eradication: area-wide pest management. *Annals of the Entomological Society of America* 91, 239–247.

Smith, J.W. and Harris, F.A. (1994) *Anthonomus* (Coleoptera: Curculionidae). In: Matthews, G.A. and Tunstall, J.P. (eds) *Insect Pests of Cotton*. Wallingford, UK: CAB International, pp. 223–258.

Smith, K.G.V. (ed.) (1973) *Insects and other Arthropods of Medical Importance*. Publication no. 720. London, UK: British Museum (Natural History).

Smith, K.G.V. (1986) *A Manual of Forensic Entomology*. London, UK: British Museum (Natural History).

Smith, M.A.H. and Lamb, R.J. (2004) Causes of variation in body size and consequences for the life history of *Sitodiplosis mosellana*. *The Canadian Entomologist* 136, 839–850.

Snyder, W.E. and Ives, A.R. (2001) Generalist predators disrupt biological control by a specialist parasitoid. *Ecology* 82, 705–716.

Soden, B.J., Wetherald, R.T. *et al.* (2002) global cooling after the eruption of Mount Pinatubo: a test of climate feedback by water vapor. *Science* 296, 727–773.

Sokal, R.R. (1985) The continuing search for order. *The American Naturalist* 126, 729–749.

Sokolovska, N., Rowe, L. *et al.* (2000) Body size in mature odonates. *Ecological Entomology* 25, 239–248.

Solbreck, C. (1986) Wing and flight muscle polymorphism in a lygaeid bug, *Horvathiolus gibbicollis*: determination and life history consequences. *Ecological Entomology* 11, 435–444.

Solomon, D.M., Glen, D.M. *et al.* (1976) Predation on overwintering larvae of codling moths (*Cydia pomonella* (L.)) by birds. *Journal of Applied Ecology* 13, 341–353.

Solomon, J.D. (1995) *Guide to Insect Borers of North American Broadleaf Trees and Shrubs*. United States Department of Agriculture, Agricultural Handbook 706, pp. 735.

Solomon, M.E. (1949) The natural control of animal populations. *Journal of Animal Ecology* 18, 1–35.

Sømme, L. (1989) Adaptations of terrestrial invertebrates to the Alpine environment. *Biological Reviews* 64, 367–407.

Sømme, L. and Block, W. (1991) Adaptations to Alpine and polar environments in insects and other arthropods. In: Lee, R.E. and Denlinger, D.L. (eds) *Insects at Low Temperature*. New York, New York, USA: Chapman and Hall, pp. 318–359.

Son, Y. and Lewis, E.E. (2005) Effects of temperature on the reproductive life history of the black vine weevil, *Otiorhynchus sulcatus*. *Entomologia Experimentalis et Applicata* 114, 15–24.

Song, S.D., Drew, R.A.I. *et al.* (2007) Multiple paternity in a natural population of a wild tobacco fly, *Bactrocera cacuminata* (Diptera: Tephritidae), assessed by microsatellite DNA markers. *Molecular Ecology* 16, 2353–2361.

Soper, R.S., Shewell, G.E. *et al.* (1976) *Calcondamyia auditrix* nov. sp. (Diptera: Sarcophagidae), a parasite which is attracted by the mating song of its host, *Okanagana rimosa* (Homoptera: Cicadidae). *The Canadian Entomologist* 108, 61–68.

Sopow, S.L. and Quiring, D.T. (1998) Body size of spruce-galling adelgids is positively related to realised fecundity in nature. *Ecological Entomology* 23, 476–479.

Soroka, J.J. and MacKay, P.A. (1990) Seasonal occurrence of the pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), on cultivars of field peas in Manitoba and its effects on pea growth and yield. *The Canadian Entomologist* 122, 1201–1210.

Soto, T. and Mogi, M. (1992) Interspecific variation in desiccation survival times of *Aedes* (*Stegomyia*) mosquito eggs in correlation with habitat and egg size. *Oecologia* 90, 353–358.

South, R. (1906) *The Butterflies of the British Isles*. London, UK: Frederick Warne.

South, R. (1920/1923) *The Moths of the British Isles*, vols. 1 and 2. London, UK: Frederick Warne.

Southgate, B.J. (1979) Biology of the Bruchidae. *Annual Review of Entomology* 24, 449–473.

Southwood, T.R.E. (1960) The abundance of Hawaiian trees and the number of their associated insect species. *Proceedings of the Hawaiian Entomological Society* 17, 299–303.

Southwood, T.R.E. (1961) The number of species of insect associated with various trees. *Journal of Animal Ecology* 30, 1–8.

Southwood, T.R.E. (1962) Migration of terrestrial arthropods in relation to habitat. *Biological Reviews* 37, 171–214.

Southwood, T.R.E. (1973) The insect/plant relationship – an evolutionary perspective. In: Van Emden, H.F. (ed.) *Insect/Plant Relationships*. Oxford, UK: Blackwell, pp. 3–30.

Southwood, T.R.E. (1977) Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46, 337–365.

Southwood, T.R.E. (1978) *Ecological Methods*, 2nd edn. London, UK: Chapman and Hall.

Southwood, T.R.E. (1985) Interactions of plants and animals: patterns and process. *Oikos* 44, 5–11.

Southwood, T.R.E. (1988) Tactics, strategies and templets. *Oikos* 52, 3–18.

Southwood, T.R.E. and Comins, H.N. (1976) A synoptic population model. *Journal of Animal Ecology* 45, 949–965.

Southwood, T.R.E. and Henderson, P.A. (2000) *Ecological Methods*, 3rd edn. Oxford, UK: Blackwell Science.

Southwood, T.R.E. and Jepson, W.F. (1962) Studies on the populations of *Oscinella frit* L. (Dipt: Chloropidae) in the oat crop. *Journal of Animal Ecology* 31, 481–495.

Southwood, T.R.E. and Way, M.J. (1970) Ecological background to pest management. In: Rabb, R.L.

and Guthrie, F.E. (eds) *Concepts of Pest Management*. Raleigh, North Carolina, USA: North Carolina State University, pp. 6–29.

Southwood, T.R.E., May, R.M. *et al.* (1974) Ecological strategies and population parameters. *The American Naturalist* 108, 791–804.

Sowig, P. (1996) Duration and benefits of biparental care in the dung beetle *Onthophagus vacca* (Coleoptera: Scarabaeidae). *Ecological Entomology* 21, 81–86.

Spalinger, D.E. and Hobbs, N.T. (1992) Mechanisms of foraging in mammalian herbivores: new models of functional response. *The American Naturalist* 140, 325–348.

Spanner, D.C. (1963) The green leaf as a heat engine. *Nature* 198, 934–937.

Sparks, T.H., Roy, D.B. *et al.* (2005) The influence of temperature on migration of Lepidoptera into Britain. *Global Change Biology* 11, 507–514.

Speight, M.R. and Wylie, F.R. (2001) *Insect Pests in Tropical Forestry*. Wallingford, UK: CABI International.

Speight, M.R., Hunter, M.D. *et al.* (1999). *Ecology of Insects*, 2nd edn. Oxford, UK: Blackwell.

Spencer, H. (1864) *The Principles of Biology*, vol. 1. London, UK: Williams and Norgate.

Spieth, H.R. and Cordes, R. (2012) Geographic comparison of seasonal migration events of the large white butterfly, *Pieris brassicae*. *Ecological Entomology* 37, 439–445.

Spradbery, J.P. (1970) Host finding in *Rhyssa persuasoria* (L.), an ichneumonid parasite of siricid woodwasps. *Animal Behaviour* 18, 103–114.

Spradbery, J.P. (1977) The oviposition biology of siricid woodwasps in Europe. *Ecological Entomology* 2, 225–230.

Sprent, J.I., Sutherland, J.M. *et al.* (1987) Some aspects of the biology of nitrogen-fixing organisms. *Philosophical Transactions of the Royal Society B* 317, 111–129.

Spurgeon, D.W. and Raulston, J.R. (2006) Captures of boll weevils (Coleoptera: Curculionidae) in traps associated with different habitats. *Journal of Economic Entomology* 99, 752–756.

Srinivasan, M.V., Zhang, S. *et al.* (2000) Honeybee navigation: nature and calibration of the "odometer". *Science* 287, 851–853.

Stamp, N. (2003a) Theory of plant defensive level: example of process and pitfalls in development of ecological theory. *Oikos* 102, 672–678.

Stamp, N. (2003b) Out of the quagmire of plant defense hypotheses. *The Quarterly Review of Biology* 78, 23–55.

Stamp, N.E. (1980) Egg deposition patterns in butterflies: why do some species cluster their eggs rather than deposit them singly? *The American Naturalist* 115, 367–380.

Stamps, J.A., Krishnan, V.V *et al.* (2005) Search costs and habitat selection by dispersers. *Ecology* 86, 510–518.

Stanton, M.L. (1982) Searching in a patchy environment: Food-plant selection by *Colias p. eriphyle* butterflies. *Ecology* 63, 839–853.

Stanton, M.L. Snow, A.A. *et al.* (1986) Floral evolution: attractiveness to pollinators influences male fitness. *Science* 232, 1625–1627.

Stanton, N.L. (1988) The underground in grassland. *Annual Review of Ecology and Systematics* 19, 573–589.

Starrfelt, J. and Kokko, H. (2010) Parent-offspring conflict and the evolution of dispersal distance. *The American Naturalist* 175, 38–49.

Starý, P. (1970) *Biology of Aphid Parasites*. The Hague, The Netherlands: Junk.

Starý, P. (1999) Parasitoids and biocontrol of Russian Wheat aphid, *Diuraphis noxia* (Kurdj.) expanding in central Europe. *Annals of Applied Entomology* 123, 273–279.

Stasek, D.J., Bean, C. *et al.* (2008) Butterfly abundance and movements among prairie patches: the roles of habitat quality, edge, and forest matrix permeability. *Environmental Entomology* 37, 897–906.

Stathers, T.E., Rees, D. *et al.* (2003) Sweet potato infestation by *Cylas* spp. in East Africa: 1. Cultivar differences in field infestation and the role of plant factors. *International Journal of Pest Management* 49, 131–140.

Stearns, S.C. (1980) A new view of life-history evolution. *Oikos* 35, 266–281.

Stearns, S.C. (1981) On measuring fluctuating environments: predictability, constancy, and contingency. *Ecology* 62, 185–199.

Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford, UK: Oxford University Press.

Stearns, S.C and Magwene, P. (2003) The naturalist in a world of genomics. *The American Naturalist* 161, 171–180.

Steck, G.J. (1991) Biochemical systematics and population genetic structure of *Anastrepha fraterculus* and related species (Diptera: Tephritidae). *Annals of the Entomological Society of America* 84, 10–19.

Stefanescu, C., Alarcón, M. *et al.* (2007) Migration of the painted lady butterfly, *Vanessa cardui*, to north-eastern Spain is aided by African wind currents. *Journal of Animal Ecology* 76, 888–898.

Stehli, F.G., Douglas, R.G. *et al.* (1969) Generation and maintenance of gradients in taxonomic diversity. *Science* 164, 947–949.

Stein, W. (1973) Zur Vererbung des Flugeldimorphismus bei *Apion virens* Herbst (Col., Curculionidae). *Zeitschrift für angewandte Entomologie* 74, 62–63.

Steinbeck, J. (1939) *The Grapes of Wrath*. New York, New York, USA: Heinemann.

Steiner, W.W.M. (1977) Niche width and genetic variation in Hawaiian *Drosophila*. *The American Naturalist* 111, 1037–1045.

Stenberg, J.A. and Hambäck, P.A. (2010) Host species critical for offspring fitness and sex ratio for an oligophagous parasitoid: implications for host co-existence. *Bulletin of Entomological Research* 100, 735–740.

Stephens, P.A., Buskirk, S.W. *et al.* (2006) Inference in ecology and evolution. *Trends in Ecology and Evolution* 22, 192–197.

Stephenson, A.G. (1981) Flower and fruit abortion: proximate causes and ultimate function. *Annual Review of Ecology and Systematics* 12, 253–279.

Stern, V.M., Smith, R.F. *et al.* (1959) The integrated control concept. *Hilgardia* 29, 81–101.

Stevens, G.C. (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist* 133, 240–256.

Stevens, P.A., Sutherland, W.J. *et al.* (1999) What is the Allee effect? *Oikos* 87, 185–190.

Stiling, P. (1987) The frequency of density dependence in insect host parasitoid systems. *Ecology* 68, 844–856.

Stiling, P. (1999) *Ecology: Theories and Applications*, 3rd edn. Upper Saddle River, New Jersey, USA: Prentice-Hall.

Stiling, P. and Rossi, A.M. (1996) Complex effects of genotype and environment on insect herbivores and their enemies. *Ecology* 77, 2212–2218.

Stinner, B.R. and House, G.J. (1990) Arthropods and other invertebrates in conservation-tillage agriculture. *Annual Review of Entomology* 35, 299–318.

Stireman, J.O., O'Hara, J.E. *et al.* (2006) Tachinidae: evolution, behavior and ecology. *Annual Review of Entomology* 51, 525–555.

Stoltz, D.B. and Vinson, S.B. (1979) Viruses and parasitism in insects. *Advances in Virus Research* 24, 125–171.

Stone, R. (1999) Coming to grips with the Aral Sea's grim legacy. *Science* 284, 30–33.

Storer, A.J., Wood, D.L. *et al.* (2004) Twig beetles, *Pityophthorus* spp. (Coleoptera: Scolytidae), as vectors of the pitch canker pathogen in California. *The Canadian Entomologist* 136, 685–693.

Storey, K.B. (1990) Biochemical adaptation for cold hardiness in insects. *Philosophical Transactions of the Royal Society B* 326, 635–654.

Stork, N.E. (1990) *The Role of Ground Beetles in Ecological and Environmental Studies*. Andover, UK: Intercept.

Stout, M.J., Thaler, J.S. *et al.* (2006) Plant-mediated interactions between pathogenic micro-organisms and herbivorous arthropods. *Annual Review of Entomology* 51, 663–689.

Stouthamer, R., Luck, R.F. *et al.* (1990) Antibiotics cause parthenogenetic *Trichogramma* (Hymenoptera; Trichogrammatidae) to revert to sex. *Proceedings of the National Academy of Sciences USA* 87, 2424–2427.

Stouthamer, R., Luck, R.F. *et al.* (1992) Genetics of sex determination and the improvement of biological control using parasitoids. *Environmental Entomology* 21, 427–435.

Stouthamer, R., Breeuwer, J.A.J. *et al.* (1993) Molecular identification of micro-organisms associated with parthenogenesis. *Nature* 361, 66–68.

Strand, M.R. and Pech, L.L. (1995) Immunological compatibility in parasitoid-host relationships. *Annual Review of Entomology* 40, 31–56.

Strathdee, A.T. and Bale, J.S. (1998) Life on the edge: insect ecology in Arctic environments. *Annual Review of Entomology* 43, 85–106.

Strathdee, A.T., Howling, G.G. *et al.* (1995) Cold hardiness of overwintering aphid eggs. *Journal of Insect Physiology* 41, 653–657.

Strauss, S.Y. (1997) Floral characteristics link herbivores, pollinators, and plant fitness. *Ecology* 78, 1640–1645.

Strauss, S.Y. and Armbruster, W.S. (1997) Linking herbivory and pollination - new perspectives on plant and animal ecology. *Ecology* 78, 1617–1618.

Straw, N.A. (1991) Resource limitation of tephritid flies on lesser burdock, *Arctium minus* (Hill) Bernh. (Compositae). *Oecologia* 86, 492–502.

Strong, D.R. (1977) Epiphyte loads, tree falls, and perennial forest disruption: a mechanism for maintaining higher tree species richness in the tropics without animals. *Journal of Biogeography* 7, 215–218.

Strong, D.R. (1980) Null hypotheses in ecology. *Synthese* 43, 271–285.

Strong, D.R. (1986) Density-vague population change. *Trends in Ecology and Evolution* 1, 39–42.

Strong, D.R. (1997) Fear no weevil? *Science* 277, 1058–1059.

Strong, D.R. and Levin, D.A. (1979) Species richness of plant parasites and growth form of their hosts. *The American Naturalist* 114, 1–22.

Strong, D.R. and Pemberton, R.W. (2000) Biological control of invading species – risk and reform. *Science* 288, 1969–1970.

Strong, D.R. and Stiling, P.D. (1983) Wing dimorphism changed by experimental density manipulation in a planthopper (*Prokelisia marginata*, Homoptera, Delphacidae). *Ecology* 64, 206–209.

Strong, D.R., McCoy, E.D. *et al.* (1977) Time and the number of herbivore species: the pests of sugarcane. *Ecology* 58, 167–175.

Strong, D.R., Lawton, J.H. *et al.* (1984) *Insects on Plants: Community Patterns and Mechanisms*. Oxford, UK: Blackwell.

Subinprasert, S. and Svensson, B.W. (1988) Effects of clutch size and egg dispersion in the codling moth *Laspeyresia pomonella*. *Ecological Entomology* 13, 87–94.

Suckling, D.M., Hackett, J.K. *et al.* (2006) Effect of irradiation on female painted apple moths, *Teia anartoides* (Lep., Lymantriidae), sterility and attractiveness to males. *Journal of Applied Entomology* 130, 167–170.

Sugg, D.W., Chesser, R.K. *et al.* (1996) Population genetics meets behavioral ecology. *Trends in Ecology and Evolution* 11, 338–342.

Sugihara, G. (1980) Minimal community structure: an explanation of species abundance patterns. *The American Naturalist* 116, 770–787.

Sullivan, D.J. (1987) Insect hyperparasitism. *Annual Review of Entomology* 32, 49–70.

Sullivan, D.J. and Völkl, W. (1999) Hyperparasitism: multitrophic ecology and behavior. *Annual Review of Entomology* 44, 291–315.

Sun, M. and Xiong, Y. (2005) Dynamic flight stability of a hovering bumble bee. *The Journal of Experimental Biology* 208, 447–459.

Sunderland, K.D. (1988) Quantitative methods for detecting invertebrate predation occurring in the field. *Annals of Applied Biology* 112, 201–224.

Sunderland, K.D., Fraser, A.M. *et al.* (1986) Field and laboratory studies on money spiders (Linyphiidae) as predators of cereal aphids. *Journal of Applied Ecology* 23, 433–447.

Sunderland, K.D., Crook, N.E. *et al.* (1987) A study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. *Journal of Applied Ecology* 24, 907–933.

Sutcliffe, O., Thomas, C.D. *et al.* (1996) Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology* 65, 85–95.

Swanson, B.J. and Johnson, D.R. (1999) Distinguishing causes of intraspecific synchrony in population dynamics. *Oikos* 86, 265–274.

Svärd L. and Wiklund, C. (1988) Fecundity, egg weight and longevity in relation to multiple matings in females of the monarch butterfly. *Behavioral Ecology and Sociobiology* 23, 39–43.

Svensson, E. *et al.* (2005) Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. *The American Naturalist* 165, 567–576.

Swanson, R., Edlund, A.F. *et al.* (2004) Species specificity in pollen-pistil interactions. *Annual Review of Genetics* 38, 793–818.

Sweeney, B.W. and Vannote, R.L. (1982) Population synchrony in mayflies: a predator satiation hypothesis. *Evolution* 36, 810–821.

Sweeny, T.L. and Barr, A.R. (1978) Sex ratio distortion caused by meiotic drive in a mosquito, *Culex pipiens* L. *Genetics* 88, 427–446.

Swetnam, T.W. (1993) Fire history and climate change in giant sequoia groves. *Science* 262, 885–889.

Sword, G.A. (1999) Density-dependent warning coloration. *Nature* 397, 217.

Szathmáry, E. and Maynard Smith, J. (1995) The major evolutionary transitions. *Nature* 374, 227–232.

Szujecki, A. (1987) *Ecology of Forest Insects*. Dordrecht, Germany: Kluwer Academic Publishers.

Tabashnik, B.E. and Mau, R.F.L. (1986) Suppression of diamondback moth (Lepidoptera: Plutellidae) oviposition by overhead irrigation. *Journal of Economic Entomology* 79, 189–191.

Tabashnik, B.E., Liu, Y-B. *et al.* (1994) One gene in diamond back moths confers resistance to four

Bacillus thuringiensis toxins. *Proceedings of the National Academy of Sciences USA* 94, 1640–1644.

Tabashnik, B.E., Liu, Y-B. *et al.* (1997) Global variation in the genetic and biochemical basis of diamondback moth resistance to *Bacillus thuringiensis*. *Proceedings of the National Academy of Sciences of the USA* 94, 12780–12785.

Taffe, C.A. (1979) The ecology of two West Indian species of mud wasps (Eumenidae: Hymenoptera). *Biological Journal of the Linnean Society* 11, 1–17.

Taffe, C.A. (1983) The biology of the mud wasp *Zeta abdominale* (Drury) (Hymenoptera: Eumenidae). *Zoological Journal of the Linnean Society* 78, 385–393.

Taffe, C.A. and Ittyeipe, K. (1976) The effect of nest substrata on the mortality of *Eumenes colona* Saussure, (Hymenoptera) and its inquilines. *Journal of Animal Ecology* 45, 303–311.

Tagawa, A., Matsushita, A. *et al.* (2008) Leaf surface preference of the cabbage worm, *Pieris rapae crucivora*, and parasitism by the gregarious parasitoid *Cotesia glomerata*. *Entomologia Experimentalis et Applicata* 129, 37–43.

Takabayashi, J. and Dicke, M. (1996) Plant-carnivore mutualism through herbivore-induced carnivore attractants. *Trends in Plant Science* 1, 109–113.

Takhtajan, A. (1969) *Flowering Plants. Origin and Dispersal*. Edinburgh, UK: Oliver and Boyd.

Takken, W., Hiscox, A. *et al.* (2015) Synthetic odour blends for sampling malarial mosquitoes. *Antenna*, Special Edition, 92–93.

Talekar, N.S. and Shelton, A.M. (1993) Biology, ecology and management of the diamondback moth. *Annual Review of Entomology* 38, 275–301.

Tammaru, T., Kaitaniemi, P. *et al.* (1996) Realised fecundity in *Epirrita autumnata* (Lepidoptera: Geometridae): relation to body size and consequences to population dynamics. *Oikos* 77, 407–416.

Tanaka, S., Nishida, T. *et al.* (2007) Sequential rapid adaptation of indigenous parasitoid wasps to the invasive butterfly *Pieris brassicae*. *Evolution* 61, 1791–1802.

Tansley, A.G. (1935) The use and abuse of vegetational concepts and terms. *Ecology* 16, 284–307.

Tansley, A.G. (1946) *Introduction to Plant Ecology*. London, UK: Unwin.

Tauber, C.A. and Tauber, M.J. (1981) Insect seasonal cycles: genetics and evolution. *Annual Review of Ecology and Systematics* 12, 281–308.

Tauber, M.J. and Tauber, C.A. (2002) Prolonged dormancy in *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae): a ten year field study with implications for crop rotation. *Environmental Entomology* 31, 499–504.

Tauber, M.J., Tauber, C.A. *et al.* (1998) Moisture, a vital but neglected factor in the seasonal ecology of insects: hypotheses and tests of mechanisms. *Environmental Entomology* 27, 523–530.

Tautz, D. and Schmid, K.J. (1998) From genes to individuals: developmental genes and the generation of the phenotype. *Philosophical Transactions of the Royal Society B* 353, 231–240.

Taylor, A.D. (1990) Metapopulations, dispersal, and predator-prey dynamics: an overview. *Ecology* 71, 429–433.

Taylor, G.K. and Krapp, H.G. (2008) Sensory systems and flight stability: what do insects measure and why? *Advances in Insect Physiology* 34, 231–316.

Taylor, L.R. (1961) Aggregation, variance and the mean. *Nature* 189, 732–735.

Taylor, L.R. (1963) Analysis of the effect of temperature on insects in flight. *Journal of Animal Ecology* 32, 99–117.

Taylor, L.R. (1974) Insect migration, flight periodicity and the boundary layer. *Journal of Animal Ecology* 43, 225–238.

Taylor, L.R. (1975) Longevity, fecundity and size; control of reproductive potential in a polymorphic migrant, *Aphis fabae* Scop. *Journal of Animal Ecology* 44, 135–163.

Taylor, L.R. (1977) Migration and the spatial dynamics of an aphid. *Journal of Animal Ecology* 46, 411–423.

Taylor, L.R. (1978) Bates, Williams, Hutchinson - a variety of diversities. *Symposia of the Royal Entomological Society* 9, 1–18.

Taylor, L.R. (1984) Assessing and interpreting the spatial distributions of insects. *Annual Review of Entomology* 29, 321–357.

Taylor, L.R. (1986) Synoptic dynamics, migration and the insect Rothamsted Survey. *Journal of Animal Ecology* 55, 1–38.

Taylor, L.R. and Taylor, R.A.J. (1977) Aggregation, migration and population mechanics. *Nature* 265, 415–421.

Taylor, L.R., French, R.A. *et al.* (1978a) The Rothamsted Insect Survey and urbanisation of land in Great Britain. In: Frankie, G.W. and Koehler, C.S. (eds) *Perspectives in Urban Entomology*. London, UK: Academic Press, pp. 31–65.

Taylor, L.R., Woiwod, I.P. *et al.* (1978b) Density-dependence of spatial behaviour and the rarity of randomness. *Journal of Animal Ecology* 47, 383–406.

Taylor, P.D. (1988) An inclusive fitness model for dispersal of offspring. *Journal of Theoretical Biology* 130, 363–378.

Taylor, R.A.J (1978) The relationship between density and distance in dispersing insects. *Ecological Entomology* 3, 63–70.

Taylor, R.A.J (1980) A family of regression equations describing the density distribution of dispersing organisms. *Nature* 286, 53–55.

Taylor, R.A.J and Reling, D. (1986a) Density/height profile and long-range dispersal of first instar gypsy moths (Lepidoptera: Lymantriidae). *Environmental Entomology* 15, 431–435.

Taylor, R.A.J and Reling, D. (1986b) Preferred wind direction of long-distance leafhopper (*Empoasca fabae*) migrants and its relevance to the return migration of small insects. *Journal of Animal Ecology* 55, 1103–1114.

Taylor, R.J. (1974) Role of learning in insect parasitism. *Ecological Monographs* 44, 89–104.

Templeton, A.R. (2001) Using phylogeographic analyses of gene trees to test species status and processes. *Molecular Ecology* 10, 779–791.

Tenczar, E.G. and Krischik, V.A. (2006) Management of cottonwood leaf beetles (Coleoptera: Chrysomelidae) with a novel transplant soak and biorational insecticides to conserve coccinellid beetles. *Journal of Economic Entomology* 99, 102–108.

Teng, P.S. (1994) Integrated pest management in rice. *Experimental Agriculture* 30, 115–137.

Terborgh, J. (1985) The vertical component of plant species diversity in temperate and tropical forests. *The American Naturalist* 126, 760–776.

Thacker, J.R.M. (2002) *An Introduction to Arthropod Pest Control*. Cambridge, UK: Cambridge University Press.

Thaler, J.S. (2002) Effect of jasmonate-induced plant responses on the natural enemies of herbivores. *Journal of Animal Ecology* 71, 141–150.

Thiele, H.U. (1977) *Carabid Beetles in their Environment*. Berlin, Germany: Springer.

Thies, C. and Tscharntke, T. (1999) Landscape structure and biological control in agro-ecosystems. *Science* 285, 893–895.

Thies, C., Steffan-Dewenter, I. *et al.* (2003) Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101, 18–25.

Thies, C., Roschewitz, I. *et al.* (2005) The landscape context of cereal aphid-parasitoid interactions. *Proceedings of the Royal Society B* 272, 203–210.

Thireau, J.C. and Regniere, J. (1995) Development, reproduction, voltinism and host synchrony of *Meteorus trachynotus* with its hosts *Choristoneura fumiferana* and *C. rosaceana*. *Entomologia Experimentalis et Applicata* 76, 67–82.

Thoday, J.M. (1953) Components of fitness. *Symposia of the Society for Experimental Biology* 7, 96–113.

Thoday, J.M. and Gibson, J.B. (1962) Isolation by disruptive selection. *Nature* 193, 1164–1166.

Thom, C., Guerenstein, P.G. *et al.* (2004) Floral CO_2 reveals flower profitability to moths. *Journal of Chemical Ecology* 30, 1285–1288.

Thomas, A.W., Borland, S.A. *et al.* (1980) Field fecundity of the spruce budworm (Lepidoptera: Tortricidae) as determined from regression relationships between egg complement, fore wing length, and body weight. *Canadian Journal of Zoology* 58, 1608–1611.

Thomas, C.D. and Kunin, W.E. (1999) The spatial structure of populations. *Journal of Animal Ecology* 68, 647–657.

Thomas, C.D., Singer, M.C. *et al.* (1996) Catastrophic extinction of population sources in a butterfly metapopulation. *The American Naturalist* 148, 957–975.

Thomas, C.D., Bodsworth, E.J. *et al.* (2001) Ecological and evolutionary processes at expanding range margins. *Nature* 411, 577–581.

Thomas, D.D., Donnelly, C.A. *et al.* (2000) Insect population control using a dominant, repressible, lethal genetic system. *Science* 287, 2474–2476.

Thomas, J.A. (1983) The ecology and status of *Thymelicus acteon* (Lepidoptera: Hesperidae) in Britain. *Ecological Entomology* 8, 427–435.

Thomas, J.A. (1995) The ecology and conservation of *Maculinea arion* and other European species of large blue butterfly. In: Pullin, A.S. (ed.) *Ecology and Conservation of Butterflies*. London, UK: Chapman and Hall, pp. 180–197.

Thomas, J.A., Clarke, R.T. *et al.* (1998) Population dynamics in the genus *Maculinea* (Lepidoptera: Lycaenidae) In: Dempster, J.P. and McLean, I.G.F. (eds) *Insect Populations in Theory and in Practice*. Dordrecht, Germany: Kluwer, pp. 261–290.

Thomas, M. and Willis, A. (1998) Biocontrol risky but necessary. *Trends in Ecology and Evolution* 13, 325–329.

Thomas, M.B., Wratten, S.D. *et al.* (1991) Creation of ‘island’ habitats in farmland to manipulate populations of beneficial arthropods: predator densities and emigration. *Journal of Applied Ecology* 28, 906–917.

Thompson, E.A. (1983) Gene extinction and allelic origins in complex genealogies. *Proceedings of the Royal Society of London B* 219, 241–251.

Thompson, J.N. (1982) *Interaction and Coevolution*. New York, New York, USA: Wiley.

Thompson, J.N. (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia Experimentalis et Applicata* 47, 3–14.

Thompson, J.N. (1997) Evaluating the dynamics of coevolution among geographically structured populations. *Ecology* 78, 1619–1623.

Thompson, J.N. (1998) Rapid evolution as an ecological process. *Trends in Ecology and Evolution* 13, 329–332.

Thompson, K. and Grime, J.P. (1988) Competition reconsidered – a reply to Tilman. *Functional Ecology* 2, 114–116.

Thompson, K.J. (1986) Oviposition digging in the grasshopper. 1. Functional anatomy and motor programme. *The Journal of Experimental Biology* 122, 387–411.

Thompson, W.R. (1922) Étude mathématique de l’action des parasites entomophages. Accroissement de la proportion d’hôtes parasites dans le parasitisme cyclique. *Compte Rendu de l’ Académie des Sciences, Paris* 174, 1201–1204, 1433–1435, 1647–1649; and 175, 65–68.

Thompson, W.R. (1924) La théorie mathématique de l’action des parasites entomophages et le facteur du hasard. *Annales de la Faculté des Sciences de Marseilles*, *Ser.* 2, 2, 69–89.

Thompson, W.R. (1929) On natural control. *Parasitology* 21, 269–281.

Thompson, W.R. (1939) Biological control and the theories of the interactions of populations. Parasitology 31, 299–388.

Thompson, W.R. (1943) *A Catalogue of the Parasites and Predators of Insect Pests*. London, UK: Imperial Parasite Service.

Thompson, W.R. (1956) The fundamental theory of natural and biological control. *Annual Review of Entomology* 1, 379–402.

Thompson, W.R. and Parker, H.L. (1927) The problem of host relations with special reference to entomophagous parasites. *Parasitology* 19, 1–34.

Thompson, W.R. and Parker, H.L. (1928a) *The European Corn Borer and its Controlling Factors in Europe*. Technical Bulletin 59, Washington, DC, USA: United States Drug Administration.

Thompson, W.R. and Parker, H.L. (1928b) Host selection in *Pyrausta nubilalis* Hübn. *Bulletin of Entomological Research* 18, 358–364.

Thomson, D.J. (1980) Implications of different sorts of evidence for competition. *The American Naturalist* 116, 719–726.

Thorne, B.L. (1997) Evolution of eusociality in termites. *Annual Review of Ecology and Systematics* 28, 27–54.

Thornhill, R. (1976) Sexual selection and paternal investment in insects. *The American Naturalist* 110, 153–163.

Thorpe, W.H. and Caudle, H.B. (1938) A study of the olfactory responses of insect parasites to the food plant of their host. *Parasitology* 30, 523–528.

Tiffany, B.H. and Mazer, S.J. (1995) Angiosperm growth habit, dispersal and diversification reconsidered. *Evolutionary Ecology* 9, 93–117.

Tikkanen, O-P., Carr, T.G. *et al.* (1999) Factors influencing the distribution of a generalist spring-feeding moth, *Operophtera brumata* (Lepidoptera: Geometridae), on host plants. *Environmental Entomology* 28, 461–469.

Tikkanen, O-P and Niemelä, P. *et al.* (2000) Growth and development of a generalist insect herbivore, *Operophtera brumata*, on original and alternative host plants. *Oecologia* 122, 529–536.

Tilman, D. (1987) The importance of the mechanisms of interspecific competition. *The American Naturalist* 129, 769–774.

Tinbergen, N. (1935) Über die Orientierung des Bienenwolfes 2: Die Bienenjagd. *Zeitschrift Vergleich Physiologie* 21, 699–716.

Tischendorf, L. and Fahrig, L. (2000) On the usage and measurement of landscape connectivity. *Oikos* 90, 7–19.

Tiwari, S., Meyer, W.L. *et al.* (2013) Induced resistance against Asian citrus psyllid, *Diaphorina citri*, by β-aminobutyric acid in citrus. *Bulletin of Entomological Research* 103, 592–600.

Toba, H.H., Paschke, J.D. *et al.* (1967) Crowding as the primary factor in the production of the agamic alate form of *Therioaphis maculata* (Homoptera:

Aphididae). *Journal of Insect Physiology* 13, 381–396.

Toepfer, S., Gu, H. *et al.* (1999) How does *Anthonomus pomorum* (Col.: Curculionidae) colonize apple orchards in early spring? *Integrated Plant Protection in Orchards Bulletin* 22, 95–97.

Toft, C.A. and Schoener, T.W. (1983) Abundance and diversity of orb spiders on 106 Bahamian islands: biogeography at an intermediate trophic level. *Oikos* 41, 411–426.

Togashi, K. (1990) Life table for *Monochamus alternatus* (Coleoptera, Cerambycidae) within dead trees of *Pinus thunbergii*. *Japanese Journal of Entomology* 58, 217–230.

Toledo, J., Rasgado, M.A. *et al.* (2006) Infection of *Anastrepha ludens* following soil applications of *Heterorhabditis bacteriophora* in a mango orchard. *Entomologia Experimentalis et Applicata* 119, 155–162.

Tomov, B.W., Bernal, J.S. *et al.* (2003) Impacts of transgenic sugarcane expressing GNA lectin on parasitism of Mexican rice borer by *Parallorhogas pyralophagus* (Marsh) (Hymenoptera: Braconidae). *Environmental Entomology* 32, 866–872.

Tougou, D., Musolin, D.L. *et al.* (2009) Some like it hot! Rapid climate change promotes changes in distribution ranges of *Nezara viridula* and *Nezara antennata* in Japan. *Entomologia Experimentalis et Applicata* 130, 249–258.

Traub, R. and Wisseman, C.L. (1974) The ecology of chigger-borne rickettsiosis (scrub typhus). *Journal of Medical Entomology* 11, 237–303.

Traynor, R.E. and Mayhew, P.J. (2005) A comparative study of body size and clutch size across the parasitoid Hymenoptera. *Oikos* 109, 305–316.

Trewavas, A. (2001) Urban myths of organic farming. *Nature* 410, 409–410.

Trewhella, K.E., Leather, S.R. *et al.* (2000) Variation in the ability of *Pinus contorta* (lodgepole pine) to feeding by three pine defoliators, *Panolis flammea*, *Neodiprion sertifer* and *Zeiraphera diniana*. *Journal of Applied Entomology* 124, 11–17.

Tripathi, S.R. and Singh, R. (1991) Population dynamics of *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae). *Insect Science and Its Application* 12, 367–374.

Tripet, F., Thiemann, T. *et al.* (2005) Effect of seminal fluids in mating between M and S forms of *Anopheles gambiae*. *Journal of Medical Entomology* 42, 596–603.

Triplehorn, C.A. and Johnson, N.F. (2005) *Borror and Delong's Introduction to the Study of Insects*, 7th edn. Belmont, California, USA: Thomson, Brooks/Cole.

Trivers, R.L. (1972) Parental investment and sexual selection. In: Campbell, B. (ed.) *Sexual Selection and the Descent of Man 1871 – 1971*. Chicago, Illinois, USA: Aldine Publishing, pp 136–179.

Trivers, R.L. (1974) Parent–offspring conflict. *American Zoologist* 14, 249–264.

Trivers, R.L. (1985) *Social Evolution*. Menlo Park, California, USA: Benjamin/Cummings.

Trivers, R.L. (2002) *Natural Selection and Social Theory*. Oxford, UK: Oxford University Press.

Trivers, R.L. (2008) Genetic conflict within the individual. Ernst Mayr Lecture. *Berlin-Brandenburgische Akademie der Wissenschaften*. 15, 163–199.

Trivers, R.L. (2011) *The Folly of Fools: the Logic of Deceit and Self Deception*. New York, New York, USA: Basic Books.

True, J.R. (2003) Insect melanism: the molecules matter. *Trends in Ecology and Evolution* 18, 640–647.

Trumble, J.T., Carson, W.G. *et al.* (1994) Economic analysis of a *Bacillus thuringiensis*-based integrated pest management program in fresh-market tomatoes. *Journal of Economic Entomology* 87, 1463–1469.

Trumble, J.T., Carson, W.G. *et al.* (1997) Economics and environmental impact of a sustainable integrated pest management program in celery. *Journal of Economic Entomology* 90, 139–146.

Trumbo, S.T. (2016) Fate of mouse carcasses in a Northern Woodland. *Ecological Entomology* 41, 737–740.

Tscharntke, T. and Brandl, R. (2004) Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology* 49, 405–430.

Tuchman, B.W. (1978) *A Distant Mirror: The Calamitous 14th Century*. London, UK: Macmillan.

Turchin, P. (1990) Rarity of density dependence or population regulation with time lags? *Nature* 344, 660–663.

Turchin, P. (1998) *Quantitative Analysis of Movement. Measuring and Modeling Population Redistribution in Animals and Plants*. Sunderland, Massachusetts, USA: Sinauer Associates.

Turchin, P. (1999) Population regulation: a synthetic view. *Oikos* 84, 153–159.

Turchin, P. (2001) Does population ecology have general laws? *Oikos* 94, 17–26.

Turchin, P. (2003) *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton, New Jersey, USA: Princeton University Press.

Turchin, P. and Batzli, G.O. (2001) Availability of food and the population dynamics of arvicoline rodents. *Ecology* 82, 1521–1534.

Turchin, P. and Ellner, S.P. (2000) Living on the edge of chaos: population dynamics of Fennoscandian voles. *Ecology* 81, 3099–3116.

Turell, M.J., O'Guinn, M.L. *et al.* (2005) Isolation of viruses from mosquitoes (Diptera: Culicidae) collected in the Amazon Basin region of Peru. *Journal of Medical Entomology* 42, 891–898.

Turelli, M. and Barton, N.H. (2004) Polygenic variation maintained by balancing selection: pleiotropy, sex-dependent allelic effects and G x E interactions. *Genetics* 166, 1053–1079.

Turelli, M. and Barton, N.H. (2006) Will population bottlenecks and multilocus epistasis increase additive genetic variance? *Evolution* 60, 1763–1776.

Turelli, M. and Hoffmann, A.A. (1999) Microbe-induced cytoplasmic incompatibility as a mechanism for introducing transgenes into arthropod populations. *Insect Molecular Biology* 8, 243–255.

Turelli, M. and Orr, H.A. (2000) Dominance, epistasis and the genetics of postzygotic isolation. *Genetics* 154, 1663–1679.

Turelli, M., Barton, N.H. *et al.* (2001) Theory and speciation. *Trends in Ecology and Evolution* 16, 330–343.

Turlings, T.C.J., Loughrin, J.H. *et al.* (1995) How caterpillar-damaged plants protect themselves by attracting parasitic wasps. *Proceedings of the National Academy of Sciences USA* 92, 4169–4174.

Turlure, C., Legrand, D. *et al.* (2016) Male disguised females: costs and benefits of female-limited dimorphism in a butterfly. *Ecological Entomology* 41, 572–581.

Turnbull, M.W. and Webb, B.A. (2002) Perspectives on polydnavirus origin and evolution. *Advances in Virus Research* 58, 203–254.

Turner, B.D. (1983) Annual respiration and production estimates for collembolan and psocopteran epiphyte herbivores on larch trees in southern England. *Ecological Entomology* 8, 213–228.

Turner, C.E., Pemberton, R.W. *et al.* (1987) Host utilization of native *Cirsium* thistles (Asteraceae) by the introduced weevil *Rhinocyllus conicus* (Coleoptera: Curculionidae) in California. *Environmental Entomology* 16, 111–115.

Turner, G.F. and Burrows M.T. (1995) A model of sympatric speciation by sexual selection. *Proceedings of the Royal Society B* 260, 287–292.

Turner, J.R.G. (1987) The evolutionary dynamics of Batesian and Mullerian mimicry: similarities and differences. *Ecological Entomology* 12, 81–95.

Turner, J.R.G., Gatehouse, C.M. *et al.* (1987) Does solar energy control organic diversity? Butterflies, moths and British climate. *Oikos* 48, 195–205.

Turner, J.S. (2000) *The Extended Organism*. Cambridge, Massachusetts, USA: Harvard University Press.

Turnock, W.J. (1972) Geographical and historical variability in population patterns and life systems of the larch sawfly (Hymenoptera: Tenthredinidae). *The Canadian Entomologist* 104, 1883–1900.

Turnock, W.J. (1978) Egg production, oviposition behavior, and sex ratios of *Bessa harveyi* (Diptera: Tachinidae) parasitizing the larch sawfly, *Pristiphora erichsonii* (Hymenoptera: Tenthredinidae). *The Canadian Entomologist* 110, 949–956.

Turnock, W.J., and Fields, P.G. (2005) Winter climates and cold hardiness in terrestrial insects. *European Journal of Entomology* 102, 561–576.

Turnock, W.J., Boivin, G. *et al.* (1998) Interpopulation differences in the cold hardiness of *Delia radicum* (Diptera: Anthomyiidae). *The Canadian Entomologist* 130, 119–129.

Ueno, T. and Tanaka, T. (1996) Self-host discrimination by a parasitic wasp: the role of short-term memory. *Animal Behaviour* 52, 875–883.

Uesugi, A. (2015) The slow-growth high-mortality hypothesis: direct experimental support in a leaf-mining fly. *Ecological Entomology* 40, 221–228.

Uhl, C. and Kauffman, J.B. (1990) Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* 71, 437–449.

Ullyett, G.C. (1947) Mortality factors in populations of *Plutella maculipennis* Curtis (Tineidae; Lepidoptera) and their relation to the problem of control. *Memoirs of the Department of Agriculture and Forestry of South Africa* 2(6), 77–202.

Ulmer, B.J. and Dosdall, L.M. (2006) Spring emergence biology of the cabbage seedpod weevil (Coleoptera: Curculionidae). *Annals of the Entomological Society of America* 99, 64–69.

Unnithan, G.C. and Paye, S.O. (1990) Factors involved in mating, longevity, fecundity and egg fertility in the maize stem-borer, *Busseola fusca* (Fuller) (Lep., Noctuidae). *Journal of Applied Entomology* 109, 295–301.

Unruh, T.R. and Luck, R.F. (1987) Deme formation in scale insects: a test with the pinyon needle scale and a review of other evidence. *Ecological Entomology* 12, 439–449.

Unwin, D.M. (1980) *Microclimate Measurement for Ecologists*. London, UK: Academic Press.

Usherwood, J.R. and Ellington, C.P. (2002) The aerodynamics of revolving wings. 1. Model hawk moth wings. *The Journal of Experimental Biology* 205, 1547–1564.

Utida, S. (1957) Cyclic fluctuations of population density intrinsic to the host parasite system. *Ecology* 38, 442–449.

Utida, S. (1972) Density dependent polymorphism in the adult of *Callosobruchus maculatus* (Coleoptera, Bruchidae). *Journal of Stored Products Research* 8, 111–126.

Utsumi, S. and Ohgushi, T. (2008) Host plant variation in plant-mediated indirect effects: moth boring-induced susceptibility of willows to a specialist leaf beetle. *Ecological Entomology* 33, 250–260.

Uvarov, B.P. (1931) Insects and climate. *Transactions of the Entomological Society of London* 79, 1–247.

Uvarov, B.P. (1977) *Grasshoppers and Locusts*, vol. 2. London, UK: Centre for Overseas Pest Research.

Vainio, J. and Cutts, F. (1998) *Yellow Fever*. Geneva, Switzerland: WHO (WHO/EPI/GEN/98.11).

Vale, G.A., Lovemore, D.F. *et al.* (1988) Odour-baited targets to control tsetse flies, *Glossina* spp. (Diptera: Glossinidae), in Zimbabwe. *Bulletin of Entomological Research* 78, 31–49.

Valigurová, A., Michalková, V. *et al.* (2014) penetration and encapsulation of the larval endoparasitoid *Exorista larvarum* (Diptera: Tachinidae) in the factitious host *Galleria mellonella* (Lepidoptera: Pyralidae). *Bulletin of Entomological Research* 104, 203–212.

Valladares, F. and Niinemets, U. (2008) Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology and Systematics* 39, 237–257.

Valladares, G. and Lawton, J.H. (1991) Host-plant selection in the holly leaf miner: does mother know best? *Journal of Animal Ecology* 60, 227–240.

Vallin, A., Jakobsson, S. *et al.* (2005) Prey survival by predator intimidation: an experimental study of peacock butterfly defence against blue tits. *Proceedings of the Royal Society B* 272, 1203–1207.

Valovage, W.D. and Kulman, H.M. (1986) Life table of *Bessa harveyi* (Diptera: Tachinidae) parasitizing *Pikonema alaskensis* (Hymenoptera: Tenthredinidae). *Environmental Entomology* 15, 246–250.

Van Alphen, J.J.M. and Nell, H.W. (1982) Superparasitism and host discrimination by *Asobara tabida* Nees (Braconidae: Alysiinae), larval parasitoid of Drosophilidae. *Netherlands Journal of Zoology* 32, 232–260.

Van Alphen, J.J.M. and Vet, L.E.M. (1986) An evolutionary approach to host finding and selection. In: Waage, J.K. and Greathead, D.J. (eds) *Insect Parasitoids*. London, UK: Academic Press, pp. 23–61.

Van Alphen, J.J.M. and Visser, M.E. (1990) Superparasitism as an adaptive strategy for insect parasitoids. *Annual review of Entomology* 35, 59–79.

Vandel, A. (1965) *Biospeleology: The Biology of Cavernicolous Animals*. Translated from French by B.E. Freeman. Oxford, UK: Pergamon Press.

Van den Berg, J. (2006) Oviposition preference and larval survival of *Chilo partellus* (Lepidoptera: Pyralidae) on Napier grass (*Pennisetum purpureum*) trap crops. *International Journal of Pest Management* 52, 39–44.

Van den Bosch, R., Messenger, P.S. *et al.* (1982) *An Introduction to Biological Control*. New York, New York, USA: Plenum Press.

Van der Heijden, M.G.A., Kilronomos, J.N. *et al.* (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396, 69–72.

Van der Plank, J.E. (1963) *Plant Diseases: Epidemics and Control*. New York, New York, USA: Academic Press.

Van der Putten, W.H., Vet, L.E.M. *et al.* (2001) Linking above- and below-ground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. *Trends in Ecology and Evolution* 16, 547–554.

Vandermeer, J. (1982) To be rare is to be chaotic. *Ecology* 63, 1167–1168.

van Dijk, T.S. (1994) On the relationship between food, reproduction and survival in two carabid beetles. *Ecological Entomology* 19, 263–270.

van Dijk, T.S. and den Boer, P.J. (1992) The life histories and population dynamics of two carabid species on a Dutch heathland. 1. Fecundity and mortality of the juvenile stages. *Oecologia* 90, 340–352.

van Dongen, S., Backeljau, T. *et al.* (1997) Synchronisation of hatching date with budburst of individual host trees (*Quercus robur*) in the winter moth (*Operophtera brumata*) and its fitness consequences. *Journal of Animal Ecology* 66, 113–121.

van Driesche, R.G. (1983) The meaning of "percent parasitism" in studies of insect parasitoids. *Environmental Entomology* 12, 1611–1622.

van Driesche, R.G. and Bellows, T.S. (1996) *Biological Control*. New York, New York, USA: Chapman and Hall.

van Driesche, R.G., Bellows, T.S. *et al.* (1991) The meaning of percentage parasitism revisited: solutions to the problem of accurately estimating total losses from parasitism. *Environmental Entomology* 20, 1–7.

van Emden, F.I. (1954) Diptera: Tachinidae. In: *Handbooks for the Identification of British Insects* Pt 4 (a). St Albans, UK: The Royal Entomological Society, pp. 7–96.

van Emden, H.F. (1965) The role of uncultivated land in the biology of crop pests and beneficial insects. *Scientific Horticulture* 17, 121–136.

van Emden, H.F. (1966) Plant insect relationships and pest control. *World Review of Pest Control* 5, 115–123

van Emden, H.F. (1999) Transgenic host plant resistance to insects: some reservations. *Annals of the Entomological Society of America* 92, 788–797.

van Emden, H.F. and Peakall, D.B. (1996) *Beyond Silent Spring - Integrated Pest Management and Chemical Safety*. London, UK: Chapman and Hall.

van Emden, H.F. and Service, M.W. (2004) *Pest and Vector Control*. Cambridge, UK: Cambridge University Press.

van Emden, H.F. and Williams, G.F. (1974) Insect stability and diversity in agro-ecosystems. *Annual Review of Entomology* 19, 445–475.

van Emden, H.F., Douloumpaka, S. *et al.* (2015) Does the aphid parasitoid *Aphidius colemani* "immunise" its progeny against the toxic plant allelochemicals that they are likely to encounter in their aphid host? *Antenna*, (Special Edition, 2015), 51–52.

Vane-Wright, R.I. (1980) On the definition of mimicry. *Biological Journal of the Linnean Society* 13, 1–6.

Vane-Wright, R.I. (2014) What is life? And what might be said of the role of behaviour in its evolution? *Biological Journal of the Linnean Society* 112, 219–241.

Vane-Wright, R.I. and Ackery, P.R. (eds) (1984) *The Biology of Butterflies*. Symposium of the Royal Entomological Society of London, No. 11. London, UK: Academic Press.

van Huizen, T.H.P. (1977) The significance of flight activity in the life cycle of *Amara plebeja* Gyll. (Coleoptera, Carabidae). *Oecologia* 29, 27–41.

van Lenteren, J.C., Bale, J. *et al.* (2006) Assessing risks of releasing exotic biological control agents of arthropod pests. *Annual Review of Entomology* 51, 609–634.

van Nouhuys, S. and Hanski, I. (2000) Apparent competition between parasitoids mediated by a shared hyperparasitoid. *Ecological Letters* 3, 82–84.

van Nouhuys, S. and Hanski, I. (2002) Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. *Journal of Animal Ecology* 71, 639–650.

van Nouhuys, S. and Kaartinen, R. (2008) A parasitoid wasp uses landmarks while monitoring potential resources. *Proceedings of the Royal Society B* 275, 377–385.

van Nouhuys, S. and Laine, A-L. (2008) Population dynamics and sex ratio of a parasitoid altered by fungal-infected diet of host butterfly. *Proceedings of the Royal Society B* 275, 787–795.

van Nouhuys, S. and Lei, G. (2004) Parasitoid-host population dynamics: the causes and consequences of phenological asynchrony. *Journal of Animal Ecology* 73, 526–535.

van Swaay, C., Warren, M. *et al.* (2006) Biotope use and trends of European butterflies. *Journal of Insect Conservation* 10, 189–209.

van Valen, L. (1960) Further competitive exclusion. *Science* 132, 1674–1675.

van Valen, L. (1973) A new evolutionary law. *Evolutionary Theory* 1, 1–30.

van Veen, F.J.F., Morris, R.J. *et al.* (2006) Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology* 51, 187–201.

van Vianen, A. and van Lenteren, J.C. (1986) The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelininae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). 15. Oogenesis and oviposition of *Encarsia formosa*. *Journal of Applied Entomology* 102, 130–139.

van Vugt, J.J.F.A., De Jong, H. *et al.* (2009) The origin of a selfish B chromosome triggering paternal sex ratio in the parasitoid wasp *Trichogramma kaykai*. *Proceedings of the Royal Society B* 276, 4149–4154.

Varkonyi, G., Hanski, I. *et al.* (2002) Host parasitoid dynamics in periodic boreal moths. *Oikos* 98, 421–430.

Varley, G.C. (1941) On the search for hosts and the egg distribution of some chalcid parasites of the knapweed gall fly. *Parasitology* 33, 47–66.

Varley, G.C. (1947) The natural control of population balance in the knapweed gall fly (*Urophora jaceana*). *Journal of Animal Ecology* 16, 139–187.

Varley, G.C. (1949) Population changes in German forest pests. *Journal of Animal Ecology* 18, 117–122.

Varley, G.C. (1959) The biological control of agricultural pests. *Journal of the Royal Society of Arts* 107, 475–490.

Varley, G.C. and Gradwell, G.R. (1960) Key factors in population studies. *Journal of Animal Ecology* 29, 399–401.

Varley, G.C. and Gradwell, G.R. (1968) Population models for the winter moth. In: Southwood, T.R.E. (ed.) *Insect Abundance*. Oxford, UK: Blackwell, pp. 132–142.

Varley, G.C. and Gradwell, G.R. (1970) Recent advances in insect population dynamics. *Annual Review of Entomology* 15, 1–23.

Varley, G.C., Gradwell, G.R. *et al.* (1973) *Insect Population Ecology: an Analytical Approach*. Oxford, UK: Blackwell.

Vasconcelos, H.L. and Casimiro, A.B. (1997) Influence of *Azteca alfari* ants on the exploitation of *Cecropia* trees by a leaf-cutting ant. *Biotropica* 29, 84–92.

Vega, F., Benavides, P. *et al.* (2002) *Wolbachia* infection in the coffee berry borer (Coleoptera: Scolytidae). *Annals of the Entomological Society of America* 95, 374–378.

Venette, R.C. and Hutchison, W.D. (1999) Assessing the risk of establishment by pink bollworm (Lepidoptera: Gelechiidae) in the southeastern United States. *Environmental Entomology* 28, 445–455.

Venzon, M., Janssen, A. *et al.* (2000) Prey preference and reproductive success of the generalist predator *Orius laevigatus*. *Oikos* 97, 116–124.

Vercruysse, J. (1985) Estimation of the survival rate of *Anopheles arabiensis* in an urban area (Pikine - Senegal). *Journal of Animal Ecology* 54, 343–350.

Verhulst, P.F. (1838) Notice sur la loi que la population suit dans son accroissement. *Correspondances Mathematiques et Physiques* 10, 113–121.

Vermeij, G.J. (1994) The evolutionary interaction among species: selection, escalation, and coevolution. *Annual Review of Ecology and Systematics* 25, 219–236.

Verner, J. (1965) Selection for the sex ratio. *The American Naturalist* 99, 419–422.

Vernon, R.S., Kabaluk, J.T. *et al.* (2003) Aggregation of *Agriotes obscurus* (Coleoptera: Elateridae) at cereal bait stations in the field. *The Canadian Entomologist* 135, 379–389.

Vet, L.E.M. and Dicke, M. (1992) Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology* 37, 141–172.

Via, S. (2001) Sympatric speciation in animals: the ugly duckling grows up. *Trends in Ecology and Evolution* 16, 381–390.

Via, S. (2009) Natural selection in action during speciation. *Proceedings of the National Academy of Sciences of the United States of America* 106, 9939–9946.

Via, S., Bouck, A.C. *et al.* (2000) Reproductive isolation between divergent races of pea aphids on two hosts: selection against migrants and hybrids in the parental environments. *Evolution* 54, 1626–1637.

Vickerman, G.P. (1982a) Distribution and abundance of cereal aphid parasitoids (*Aphidius* spp.) on grassland and winter wheat. *Annals of Applied Biology* 101, 185–190.

Vickerman, G.P. (1982b) Distribution and abundance of adult *Opomyza florum* (Diptera: Opomyzidae) in cereal crops and grassland. *Annals of Applied Biology* 101, 441–447.

Vidal, S., Kuhlmann, U. *et al.* (2005) *Western Corn Rootworm: Ecology and Management*. Wallingford, UK: CAB International.

Villani, M.G. and Wright, R.J. (1988) Entomogenous nematodes as biological control agents for

European chafer and Japanese beetle (Coleoptera: Scarabaeidae) larvae infesting turf grass. *Journal of Economic Entomology* 81, 484–487.

Vincent, C., Hallman, G. *et al*. (2003) Management of agricultural insects with physical control methods. *Annual Review of Entomology* 48, 261–281.

Vinogradov, A.E. (2003) Selfish DNA is maladaptive: evidence from the plant Red list. *Trends in Genetics* 19, 609–614.

Vinogradov, A.E. (2004) Genome size and extinction risk in vertebrates. *Proceedings of the Royal Society B* 271, 1701–1705.

Vinogradova, E.B. (1974) The pattern of reactivation of diapausing larvae in the blow fly *Calliphora vicina*. *Journal of Insect Physiology* 20, 2487–2496.

Vinson, S.B. (1976) Host selection by insect parasitoids. *Annual Review of Entomology* 21, 109–133.

Vinson, S.B. (1984) How parasitoids locate their host: a case of insect espionage. In: Lewis, T. (ed.) *Insect Communication*. London, UK: Royal Entomological Society, pp. 325–348.

Virdee, S.R. and Hewitt, G.M. (1994) Clines for hybrid dysfunction in a grasshopper hybrid zone. *Evolution* 48, 392–407.

Vitousek, P.M. (1992) Global environmental change: an introduction. *Annual Review of Ecology and Systematics* 23, 1–14.

Vittum, P.J. (1984) Effect of lime applications on Japanese beetle (Coleoptera: Scarabaeidae) grub populations in Massachusetts soils. *Journal of Economic Entomology* 77, 687–690.

Völkl, W. (1992) Aphids or their parasitoids: who actually benefits from ant-attendance. *Journal of Animal Ecology* 61, 273–281.

Vollrath, F. and Selden, P. (2007) The role of behavior in the evolution of spiders, silks, and webs. *Annual Review of Ecology and Systematics* 38, 819–846.

Volterra, V. (1926) Fluctuations in the abundance of a species considered mathematically. *Nature* 118, 558–560.

von Frisch, K. (1967/1993) *The Dance Language and Orientation of Bees*. Cambridge, Massachusetts, USA: Harvard University Press.

Von Hassel, G. (1925) Das Geheimniss des Urwaldes. *Anzeiger für Schadlingskunde* 1, 42–43.

Vorwerk, S. and Forneck, A. (2006) Reproductive mode of grape phylloxera (*Daktulosphaira vitifoliae*, Homoptera: Phylloxeridae) in Europe: molecular evidence for predominantly asexual populations and the lack of gene flow between them. *Genome* 49, 678–687.

Voute, A.D. (1946) Regulation of the density of insect populations in virgin forests and cultivated woodlands. *Archivas Neerlanddaises de Zoologie* 7, 435–470.

Waage, J.K. (1979) The evolution of insect/vertebrate associations. *Biological Journal of the Linnean Society* 12, 187–224.

Waage, J.K. (1982) Sex ratio and population dynamics of natural enemies – some possible interactions. *Annals of Applied Biology* 101, 159–164.

Waage, J.K. (1983) Aggregation in field parasitoid populations: foraging time allocation by a population of *Diadegma* (Hymenoptera, Ichneumonidae). *Ecological Entomology* 8, 447–453.

Waage, J.K. (1986) Family planning in parasitoids: adaptive patterns of progeny and sex allocation. In: Waage, J.K. and Greathead, D.J. (eds) *Insect Parasitoids*. London, UK: Academic Press, pp. 63–95.

Waage, J.K. and Greathead, D. J. (eds) (1986) *Insect Parasitoids*. London, UK: Academic Press.

Wäckers, F.L., Romeis, J. *et al*. (2007) Nectar and pollen feeding by insect herbivores and implications for multitrophic interactions. *Annual Review of Entomology* 52, 301–323.

Wada, T., Seino, H. *et al*. (1987) Evidences of autumn overseas migration in the rice planthoppers, *Nilaparvata lugens* and *Sogatella furcifera*: analysis of light trap catches and associated weather patterns. *Ecological Entomology* 12, 321–330.

Waddington, C.H. (1957) *The Strategy of the Genes*. London, UK: Allen and Unwin.

Wade, M.J. and Goodnight, C.J. (1991) Wright's shifting balance theory: an experimental study. *Science* 253, 1015–1018.

Wagner, A. (1996) Does evolutionary plasticity evolve? *Evolution* 50, 1008–1023.

Wagner, G.P. and Altenberg, L. (1996) Complex adaptations and the evolution of evolvability. *Evolution* 50, 967–976.

Wagner, M.R., Atuahene, S.K.N. *et al*. (1991) *Forest Entomology in West Tropical Africa: Forest Insects of Ghana*. Dordrecht, Germany: Kluwer Academic Publishers.

Wajnberg, E., Scott, J.K. *et al*. (2001) *Evaluating Indirect Ecological Effects of Biological Control*. Wallingford, UK: CAB International.

Waldbauer, G.P. and Friedman, S. (1991) Self-selection of optimal diets by insects. *Annual Review of Entomology* 36, 43–63.

Walde, S.J. and Murdoch, W.W. (1988) Spatial density dependence in parasitoids. *Annual Review of Entomology* 33, 441–466.

Walde, S.J., Luck, R.F. *et al*. (1989) A refuge for red scale: the role of size-selectivity by a parasitoid wasp. *Ecology* 70, 1700–1706.

Walker, T.J. (1991) Butterfly migration from and to peninsular Florida. *Ecological Entomology* 16, 241–252.

Wall, R. and Begon, M. (1985) Competition and fitness. *Oikos* 44, 356–360.

Wallace, A.R. (1865) On the phenomena of variation and geographical distribution as illustrated by the Papilionidae of the Malayan region. *Transactions of the Linnean Society* 25, 1–71.

Wallace, A.R. (1878) *Tropical Nature and Other Essays*. London, UK: Macmillan.

Wallace, A.R. (1888) On the tendency of varieties to depart indefinitely from the original type. *Journal of the Proceedings of the Linnean Society (Zoology)* 3, 53–62.

Wallin, H. (1986) Habitat choice of some field-inhabiting carabid beetles (Coleoptera: Carabidae) studied by recapture of marked individuals. *Ecological Entomology* 11, 457–466.

Wallin, H., Chiverton, P.A. *et al*. (1992) Diet, fecundity and egg size in some polyphagous predatory carabid beetles. *Entomologia Experimentalis et Applicata* 65, 129–140.

Wallner, W.E. (1987) Factors affecting insect population dynamics: differences between outbreak and non-outbreak species. *Annual Review of Entomology* 32, 317–340.

Waloff, N. (1980) Studies on grassland leafhoppers (Homoptera: Auchenorrhyncha) and their natural enemies. *Advances in Ecological Research* 11, 81–215.

Waloff, Z. (1963) Field studies on solitary and transiens desert locusts in the Red Sea area. *Anti-locust Bulletin* 40, 1–93.

Waloff, Z. (1972) Orientation of flying locusts in migrating swarms. *Bulletin of Entomological Research* 62, 1–72.

Walter, G.H. (1988a) Activity patterns and egg production in *Coccophagus bartletti*, an aphelinid parasitoid of scale insects. *Ecological Entomology* 13, 95–105.

Walter, G.H. (1988b) Competitive exclusion, coexistence and community structure. *Acta Biotheoretica* 37, 281–313.

Walter, G.H. (2003) *Insect Pest Management and Ecological Research*. Cambridge, UK: Cambridge University Press.

Walter, G.H., Hulley, P.E. *et al*. (1984) Speciation, adaptation and interspecific competition. *Oikos* 43, 246–248.

Walter, H. (1971) *Ecology of Tropical and Subtropical Vegetation*. English edn, translated by Mueller-Dombois, D.. Edinburgh: Oliver and Boyd.

Walter, J., Meixler, M.S. *et al*. (2015) How topography induces reproductive asynchrony and alters gypsy moth invasion dynamics. *Journal of Animal Ecology* 84, 188–198.

Walton, C., Handley, J.M. *et al*. (2001) Genetic population structure and introgression in *Anopheles dirus* mosquitoes in South-east Asia. *Molecular Ecology* 10, 569–580.

Walton, M.P., Loxdale, H.D. *et al*. (2011) Flying with a "death sentence" on board: electrophoretic detection of braconid parasitoid larvae in migrating winged grain aphids, *Sitobion avenae* (F.). *Bulletin of Entomological Research* 101, 443–449.

Wand, S.J.E., Midgely, G.F. *et al*. (1999) Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO2 concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology* 5, 723–741.

Wang, H., Ando, N. *et al*. (2008) Active control of free flight manoeuvres in a hawk moth, *Agrius convolvuli*. *The Journal of Experimental Biology* 211, 423–432.

Wang, Q., Millar, J.G. *et al*. (2008) Development of a strategy for the selective collection of a parasitoid attacking one member of a large herbivore guild. *Journal of Economic Entomology* 101, 1771–1778.

Ward, K.E. and Landholt, P.J. (1995) Influence of multiple matings on fecundity and longevity of female cabbage looper moths (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America* 88, 768–772.

Ward, S.A., Leather, S.R. *et al*. (1998) Mortality during dispersal and the cost of host-specificity in parasites: how many aphids find hosts? *Journal of Animal Ecology* 67, 763–773.

Wardle, A.R. and Borden, J.H. (1985) Age-dependent associative learning by *Exeristes roborator* (F.) (Hymenoptera: Ichneumonidae). *The Canadian Entomologist* 117, 605–616.

Wardle, D.A., Bardgett, R.D. *et al.* (2004) Ecological linkages between above ground and below ground biota. *Science* 304, 1629–1633.

Warren, J.H., Raup, M.J. *et al.* (1992) Host plants used by gypsy moths affect survival and development of the parasitoid *Cotesia melanoscela*. *Environmental Entomology* 21, 173–177.

Watanabe, M. (1981). Population dynamics of the swallowtail butterfly *Papilio xuthus* L., in a deforested area. *Research in Population Ecology* 23, 74–93.

Watkinson, A.R. and Sutherland, W.J. (1995) Sources, sinks and pseudosinks. *Journal of Animal Ecology* 64, 126–130.

Watmough, R.H. (1983) Mortality, sex-ratio and fecundity in natural populations of large carpenter bees (*Xylocopa* spp.) *Journal of Animal Ecology* 52, 111–125.

Watson, M.A. and Casper, B.B. (1984) Morphogenetic constraints on patterns of carbon distribution in plants. *Annual Review of Ecology and Systematics* 15, 233–258.

Watt, A.D. and McFarlane, A.M (2002) Will climate change have a different impact on different trophic levels? Phenological development of winter moth *Operophtera brumata* and its host plants. *Ecological Entomology* 27, 254–256.

Watt, A.D. and Woiwod, I.P. (1999) The effect of phenological asynchrony on population dynamics: analysis of fluctuations of British macrolepidoptera. *Oikos* 87, 411–416.

Watt, W.B. (1992) Eggs, enzymes, and evolution: natural genetic variants change insect fecundity. *Proceedings of the National Academy of Sciences of the USA* 89, 10608–10612.

Watt, W.B. (2000) Avoiding paradigm-based limits to knowledge of evolution. *Evolutionary Biology* 32, 73–96.

Watt, W.B., Wheat, C.W. *et al.* (2003) Adaptation at specific loci. 7. Natural selection, dispersal and the diversity of molecular-functional variation patterns among butterfly species complexes (Colias: Lepidoptera, Pieridae). *Molecular Ecology* 12, 1265–1275.

Waxman, D. and Peck, J.R. (1999) Sex and adaptation in a changing environment. *Genetics* 153, 1041–1053.

Way, M.J. (1966) The natural environment and integrated methods of pest control. *Journal of Applied Ecology* 3 (Suppl.), 29–32.

Way, M.J., Cammell, M.E. *et al.* (1981) The use of egg counts and suction-trap samples to forecast the infestation of spring-sown field beans, *Vicia faba,* by the black bean aphid, *Aphis fabae*. *Annals of Applied Biology* 98, 21–34.

Weaver, S.C., Ferro, C. *et al.* (2004) Venezuelan equine encephalitis. *Annual Review of Entomology* 49, 141–174.

Webb, R.E., Ridgeway, R.L. *et al.* (1991) Development of a specialized gypsy moth (Lepidoptera: Lymantriidae) management program for suburban parks. *Journal of Economic Entomology* 84, 1320–1328.

Weeks, E.N.I. and Cordon-Rosales, C. (2013) Risk factors for domestic infestation by the Chagas' disease vector, *Triatoma dimidiata*, in Chiquimula, Guatemala. *Bulletin of Entomological Research* 103, 634–643.

Weertman, J. (1976) Milankovitch solar radiation variations and ice age ice sheet sizes. *Nature* 261, 17–20.

Wei, S-G., Wang, R. *et al.* (2002) Release of *Osmia excavata* and *Osmia jaconti* (Hymenoptera: Megachilidae) for apple pollination. *The Canadian Entomologist* 134, 369–380.

Weintraub, P.G. and Beanland, L. (2006) Insect vectors of phytoplasmas. *Annual Review of Entomology* 51, 91–111.

Weiss, S.B. and Murphy, D.D. (1988) Fractal geometry and caterpillar dispersal. *Functional Ecology* 2, 116–118.

Weiss, S.B., Murphy, D.D. *et al.* (1988) Sun, slope, and butterflies: topographic determinants of habitat quality for Euphydryas editha. *Ecology* 69, 1486–1496.

Weisser, W.W. (2000) Metapopulation dynamics in an aphid-parasitoid system. *Entomologia Experimentalis et Applicata* 97, 83–92.

Weisser, W.W. and Hassell, M.P. (1996) Animals "on the move" stabilise host/parasitoid systems. *Proceedings of the Royal Society B* 263, 749–754.

Weisser, W.W. and Houston, A.I. (1993) Host discrimination in parasitic wasps: when is it advantageous? *Functional Ecology* 7, 27–39.

Weisser, W.W., Volkl, W. *et al.* (1997) The importance of adverse weather conditions for behaviour and population ecology of an aphid parasitoid. *Journal of Animal Ecology* 66, 386–400.

Wellings, P.W. (1987) Spatial distribution and interspecific competition. *Ecological Entomology* 12, 359–362.

Wellings, P.W., Chambers, R.J. *et al.* (1985) Sycamore aphid numbers and population density. 1. Some patterns. *Journal of Animal Ecology* 54, 411–424.

Wellington, W.G. (1948) The light reactions of the spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae). *The Canadian Entomologist* 80, 56–82.

Wellington, W.G, (1954) Atmospheric circulation processes and insect ecology. *The Canadian Entomologist* 86, 312–333.

Wellington, W.G. (1957) Individual difference as a factor in population dynamics: the development of a problem. *Canadian Journal of Zoology* 35, 293–323.

Wellington, W.G. (1960) Qualitative changes in natural populations during changes in abundance. *Canadian Journal of Zoology* 38, 289–314.

Wellington, W.G. (1964) Qualitative changes in populations in unstable environments. *The Canadian Entomologist* 96, 436–451.

Wells, J.D. and Stevens, J.R. (2008) Application of DNA-based methods in forensic entomology. *Annual Review of Entomology* 53, 103–120.

Wells, P.H. and Wells, H. (1984) Can honey bees change foraging patterns? *Ecological Entomology* 9, 475–477.

Werling, B.P., Nyrop, J. *et al.* (2006) Spatial and temporal patterns of onion maggot adult activity and oviposition within onion fields that vary in bordering habitat. *Entomologia Experimentalis et Applicata* 118, 49–59.

Wermelinger, B., Rigling, A. *et al.* (2008) Assessing the role of bark- and wood-boring insects in the decline of Scots pine (*Pinus sylvestris*) in the Swiss Rhone valley. *Ecological Entomology* 33, 239–249.

Werner, D., Ahlborn, B. *et al.* (1992) Nodule development and nitrogen fixation in the *Rhizobium/Bradyrhizobium* system. *Proceedings of the Phytochemical Society of Europe* 33, 17–30.

Werren, J.H. (1997) Biology of *Wolbachia*. *Annual Review of Entomology* 42, 587–609.

Werren, J.H. and Windsor, D.M. (2000) *Wolbachia* infection frequencies in insects: evidence of a global equilibrium? *Proceedings of the Royal Society B* 267, 1277–1285.

Werren, J.H., Raupp, M.J. *et al.* (1992) Host plants used by gypsy moths affect survival and development of the parasitoid *Cotesia melanoscela*. *Environmental Entomology* 21, 173–177.

Weseloh, R.M. (1972) Influence of gypsy moth egg mass dimensions and microhabitat distributions on parasitization by *Ooencyrtus kuwanai*. *Annals of the Entomological Society of America* 65, 64–69.

Weseloh, R.M. (1982) Implications of the tree microhabitat preferences of *Compsilura concinnata* (Diptera: Tachinidae) for its effectiveness as a gypsy moth parasitoid. *The Canadian Entomologist* 114, 617–622.

Weseloh, R.M. and Andreadis, T.G. (2002) Detecting the titre in forest soils of spores of the gypsy moth (Lepidoptera: Lymantriidae) pathogen, *Entomophthora maimaiga* (Zygomycetes: Entomophthorales). *The Canadian Entomologist* 134, 269–279.

West, C. (1985) Factors underlying the late seasonal appearance of the lepidopterous leaf-mining guild on oak. *Ecological Entomology* 10, 111–120.

Westgarth-Smith, A.R., Leroy, S.A.G. *et al.* (2005) Mechanisms for the control of U.K. butterfly abundance by the North Atlantic Oscillation. *Antenna* 29, 257–266.

Whalon, M.E. and Croft, B.A. (1984) Apple IPM implementation in North America. *Annual Review of Entomology* 29, 435–470.

Wharton, R.A. (1993) Bionomics of the Braconidae. *Annual Review of Entomology* 38, 121–143.

Wheeler, D. (1996) The role of nourishment in oogenesis. *Annual Review of Entomology* 41, 407–431.

White, A.J., Wratten, S.D. *et al.* (1995) Habitat manipulation to enhance biological control of *Brassica* pests by hover flies. *Journal of Economic Entomology* 88, 1171–1176.

White, B.J., Collins, F.H. *et al.* (2011) Evolution of *Anopheles gambiae* in relation to humans and malaria. *Annual Review of Ecology and Systematics* 42, 111–132.

White, M.J.D. (1978) *Modes of Speciation*. San Francisco, California, USA: W.H. Freeman.

White, R.E. (2006) *Principles and Practice of Soil Science*, 4th edn. Oxford, UK: Blackwell.

White T.C.R. (1976) Weather, food and plagues of locusts. *Oecologia* 22, 119–134.

White, T.C.R. (1978) The importance of relative shortage of food in animal ecology. *Oecologia* 33, 71–86.

White, T.C.R. (1993) *The Inadequate Environment. Nitrogen and the Abundance of Animals*. Berlin, Germany: Springer.

White, T.C.R. (2001) Opposing paradigms: regulation or limitation of populations? *Oikos* 93, 148–152.

White, W.B., Lean, J. *et al.* (1997) Response of global upper ocean temperature to changing solar irradiance. *Journal of Geophysical Research* 102, 3255–3266.

Whitfield, J.B. (1998) Phylogeny and evolution of host-parasitoid relationship in the Hymenoptera. *Annual Review of Entomology* 43, 129–151.

Whitham, T.G. (1980) The theory of habitat selection: examined and extended using *Pemphigus* aphids. *The American Naturalist* 115, 449–466.

Whitham, T.G. and Slobodchikoff, C.N. (1981) Evolution by individuals, plant-herbivore interactions, and mosaics of genetic variability: the adaptive significance of somatic mutations. *Oecologia* 49, 287–292.

Whitman, D.W. and Agrawal, A.A. (2009) What is phenotypic plasticity and why is it important. In: Whitman , D.W. and Ananthakrishnan, T.N. (eds) *Phenotypic Plasticity in Insects. Mechanisms and Consequences*. Boca Raton, Florida, USA: CRC Press, pp. 1–63.

Whittaker, J.B. (1971) Population changes in *Neophilaenus lineatus* (L.) (Homoptera: Cercopidae) in different parts of its range. *Journal of Animal Ecology* 40, 425–443.

Whittaker, J.B. (1985) Population cycles over a 16-year period in an upland race of *Strophingia ericae* (Homoptera: Psylloidea) on Calluna vulgaris. *Journal of Animal Ecology* 54, 311–321.

Whittaker, R.H., Levin, S.A. *et al.* (1975) On the reasons for distinguishing "Niche, habitat and ecotope". *The American Naturalist* 109, 479–482.

WHO (1998) Control and surveillance of African trypanosomiasis. *WHO technical Report Series* 851, 1–113.

Whorton, J.C. (1974) *Before Silent Spring: Pesticides and Public Health in Pre-DDT America*. Princeton, New Jersey, USA: Princeton University Press.

Wickman, P.O. and Rutowski, R.L. (1999) The evolution of mating dispersion in insects. *Oikos* 84, 463–472.

Wiens, J.A. (1976) Population responses to patchy environments. *Annual Review of Ecology and Systematics* 7, 81–120.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology* 3, 385–397.

Wiens, J. A., Crawford, C.S. *et al.* (1985) Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45, 421–427.

Wierenga, J.M., Norris, D.L. *et al.* (1996) Stage-specific mortality of Colorado potato beetles (Coleoptera: Chrysomelidae) feeding on transgenic potatoes. *Journal of Economic Entomology* 89, 1047–1052.

Wigglesworth, V.B. (1984) *The Principles of Insect Physiology*, 8th edn. London, UK: Chapman and Hall.

Wiklund, C. (1981) Generalist vs. specialist oviposition behaviour in *Papilio machaon* (Lepidoptera) and functional aspects on the hierarchy of oviposition preferences. *Oikos* 36, 163–170.

Wiklund, C. (1984) Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. *Oecologia* 63, 23–29.

Wilde, G. (1981) Wheat arthropod pest management. In: Pimentel, D. (ed.) *Handbook of Pest Management in Agriculture*. Boca Raton, Florida, USA: C.R.C. Press, pp. 317–328.

Wiley, R.H. and Poston, J (1996) Indirect mate choice, competition for mates, and co-evolution of the sexes. *Evolution* 50, 1371–1381.

Wilkinson, T.L. and Douglas, A.E. (1995) Aphid feeding, as influenced by disruption of the symbiotic bacteria: an analysis of the pea aphid (*Acyrthosiphon pisum*). *Journal of Insect Physiology* 41, 635–640.

Williams, C.B. (1947) The generic relations of species in small ecological communities. *Journal of Animal Ecology* 16, 11–18.

Williams, C.B. (1951) Intra-generic competition as illustrated by Moreau's records of East African bird communities. *Journal of Animal Ecology* 20, 246–253.

Williams, C.B. (1958) *Insect Migration*. London, UK: Collins.

Williams, C.B. (1964) *Patterns in the Balance of Nature*. London, UK: Academic Press.

Williams, D.J. and Langor, D.W. (2011) Distribution, species composition, and incidence of egg parasitoids of the forest tent caterpillar (Lepidoptera: Lasiocampidae), during a widespread outbreak in the Canadian prairies. *The Canadian Entomologist* 143, 272–278.

Williams, D.W. and Liebhold, A.M. (1997) Detection of delayed density dependence: reply. *Ecology* 78, 320–322.

Williams, D.W. and Liebhold, A.M. (2000) Spatial synchrony of spruce budworm outbreaks in eastern North America. *Ecology* 81, 2753–2766.

Williams, G.C. (1966) *Adaptation and Natural Selection*. Princeton, New Jersey, UK: Princeton University Press.

Williams, G.C. (1971) *Group Selection*. Chicago, Illinois, USA: Aldine-Atherton.

Williams, G.C. (1975) *Sex and Evolution*. Princeton, New Jersey, USA: Princeton University Press.

Williams, G.C. (1992) *Natural selection: Domains, Levels, and Challenges*. Oxford, UK: Oxford University Press.

Williams, I.H., Frearson, D.J.T. *et al*. (2007) First field evidence that parasitoids use upwind anemotaxis for host-habitat location. *Entomologia Experimentalis et Applicata* 123, 299–307.

Williams, I.S. (1999) Slow growth, high-mortality - a general hypothesis, or is it? Ecological Entomology 24, 490–495.

Williams, K.A. and Villet, M.H. (2006) A history of southern African research relevant to forensic entomology. *South African Journal of Science* 102, 59–65.

Williams, K.S. and Gilbert, L.E. (1981) Insects as selective agents on plant vegetative morphology: egg mimicry reduces egg laying by butterflies. *Science* 212, 467–469.

Williamson, M.H. (1957) An elementary theory of interspecific competition. *Nature* 180, 422–425.

Williamson, M.H. (1991) Biocontrol risks. *Nature* 353, 394.

Williamson, M.H. (1992) Environmental risks from the release of genetically modified organisms (GMOs) – the need for molecular ecology. *Molecular Ecology* 1, 3–8.

Williamson, M.H. (1996) *Biological Invasions*. London, UK: Chapman and Hall.

Williamson, M.H. and Fitter, A. (1996) The varying success of invaders. *Ecology* 77, 1661–1666.

Williamson, M.H. and Gaston, K. J. (2005) The lognormal distribution is not an appropriate null hypothesis for the species-abundance distribution. *Journal of Animal Ecology* 74, 409–422.

Willink, E. and Moore, D. (1988) Aspects of the biology of *Rastrococcus invadens* Williams (Hemiptera: Pseudococcidae), a pest of fruit crops in West Africa, and one of its primary parasitoids, *Gyranusoidea tebygi* Noyes (Hymenoptera: Encyrtidae). *Bulletin of Entomological Research* 78, 709–715.

Willis, J.C. (1922) *Age and Area*. Cambridge, UK: Cambridge University Press.

Willmer, P.G. (1982) Microclimate and the environmental physiology of insects. *Advances in Insect Physiology* 16, 1–57.

Willmer, P.G. (1983) Thermal constraints on activity patterns in nectar-feeding insects. *Ecological Entomology* 8, 455–469.

Willmer, P.G. and Stone, G.N. (1997) How aggressive ant guards assist seed-set in *Acacia* flowers. *Nature* 388, 165–167.

Willmer, P.G., Bataw, A.M. *et al*. (1994) The superiority of bumble bees to honey bees as pollinators: insect visits to raspberry flowers. *Ecological Entomology* 19, 271–284.

Willmott, A.P. and Ellington, C.P. (1997) The mechanics of flight in the hawk moth *Manduca sexta*. 2. *The Journal of Experimental Biology* 200, 2723–2745.

Wills, C. (1996) *Yellow Fever, Black Goddess*. Reading, Massachusetts, USA: Adison-Wesley.

Wilson, D.S. (1983) The group selection controversy: history and current status. *Annual Review of Ecology and Systematics* 14, 159–187.

Wilson, D.S. (1997) Biological communities as functionally organised units. *Ecology* 78, 2018–2024.

Wilson, D.S. (1998) Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society B* 353, 199–205.

Wilson, D.S., Knollenberg, W.G. *et al*. (1984) Species packing and temperature dependent competition among burying beetles (Silphidae, *Nicrophorus*). *Ecological Entomology* 9, 205–216.

Wilson, E.O. (1970) Chemical communication within animal species. In: Sondheimer, E. and Simeone, J.B. (eds) *Chemical Ecology*. New York, New York, USA: Academic Press.

Wilson, E.O (1971) *The Insect Societies*. Cambridge, Massachusetts, USA: Harvard University Press.

Wilson, E.O. (1975) *Sociobiology: The New Synthesis*. Cambridge, Massachusetts, USA: Belknap Press.

Wilson, J.R.U., Rees, M. *et al*. (2006) Population regulation of a classical biological control agent: larval density dependence in *Neochetina eichhorniae* (Coleoptera: Curculionidae), a biological control agent of water hyacinth *Eichhornia crassipes*. *Bulletin of Entomological Research* 96, 145–152.

Wimp, G.M. and Whitham, T.G. (2001) Biodiversity consequences of predation and host-plant hybridization on an ant-aphid mutualism. *Ecology* 82, 440–452.

Winder, L. (1990) Predation of the cereal aphid *Sitobion avenae* by polyphagous predators on the ground. *Ecological Entomology* 15, 105–110.

Winder, L., Griffiths, G.K.J. *et al.* (2005) The role of large-scale spatially explicit and small-scale localised processes on the population dynamics of cereal aphids. *Bulletin of Entomological Research* 95, 579–587.

Winograd, I.J., Coplen, T.B. *et al.* (1992) Continuous 500,000-year climate record from vein calcite in Devil's Hole, Nevada. *Science* 258, 255–260.

Wint, W. (1983) The role of alternative host-plant species in the life cycle of a polyphagous moth, *Operophtera brumata* (Lepidoptera: Geometridae). *Journal of Animal Ecology* 52, 439–450.

Whipple, K.X., Kirby, E. *et al.* (1999) Geomorphic limits to climate-induced increases in topographic relief. *Nature* 401, 39–43.

Withers, T.M., Madie, C. *et al.* (1997) The influence of clutch size on survival and reproductive potential of the Hessian fly, *Mayetiola destructor*. *Entomologia Experimentalis et Applicata* 83, 205–212.

Witz, B.W. (1990) Antipredator mechanisms in arthropods: a twenty year literature survey. *The Florida Entomologist* 73, 71–99.

Witzgall, P., Stelinski, L. *et al.* (2008) Codling moth management and chemical ecology. *Annual Review of Entomology* 53, 503–522.

Woiwod, I.P., Reynolds, D.R. *et al.* (eds) (2001) *Insect Movement: Mechanisms and Consequences*. Wallingford, UK: CAB International.

Wolda, H. (1978) Seasonal fluctuations in rainfall, food and abundance of tropical insects. *Journal of Animal Ecology* 47, 369–381.

Wolda, H. (1995) The demise of the population regulation controversy? *Research in Population Ecology* 37, 91–93.

Wolda, H. and Denlinger, D.L. (1984) Diapause in a large aggregation of a tropical beetle. *Ecological Entomology* 9, 217–230.

Wood, T.K. (1993) Diversity in the New World Membracidae. *Annual Review of Entomology* 38, 409–435.

Wood, T.K. and Keese, M.C. (1990) Host-plant-induced assortative mating in *Enchenopa* treehoppers. *Evolution* 44, 619–628.

Wood, T.K. and Olmstead, K.L. (1984) Latitudinal effects on treehopper species richness (Homoptera: Membracidae). *Ecological Entomology* 9, 109–115.

Woodrow, D.F. (1965) Observations on the red locust (*Nomadacris septemfasciata* Serv.) in the Rukwa Valley, Tanganyika. *Journal of Animal Ecology* 34, 187–200.

Woodson, W.R. (2002) Pollination signals and flower senescence. *Plant Reproduction. Annual Plant Reviews* 6, 279–295.

Wool, D., van Emden, H.F. *et al.* (1978) Electrophoretic detection of the internal parasite, *Aphidius matricariae* in *Myzus persicae*. *Annals of Applied Biology* 90, 21–26.

Woolhouse, M.E.J. and Harmsen, R. (1987) Just how unstable are agroecosystems? *Canadian Journal of Zoology* 65, 1577–1580.

Wootton, J.T. (1994) The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 25, 443–466.

Wootton, J.T. and Emmerson, M. (2005) Measurement of interaction strength. *Annual Review of Ecology, Evolution and Systematics* 36, 419–444.

Wootton, R.J. (1976) The fossil record and insect flight. *Symposia of the Royal Entomological Society* 7, pp. 235–254.

Wootton, R.J. (1992) Functional morphology of insect wings. *Annual Review of Entomology* 37, 113–140.

Wratten, S.D. and Powell, W. (1990) Cereal aphids and their natural enemies. In: Firbank, L.G., Carter, N. *et al.* (eds) *The Ecology of Temperate Cereal Fields*. London, UK: Blackwell, pp. 233–257.

Wratten, S.D., Bowie, M.H. *et al.* (2003) Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. *Oecologia* 134, 605–611.

Wright, D.H. (1983) Species-energy theory: an extension of species area theory. *Oikos* 41, 496–506.

Wright, G.J. and Rayner, J.C. (2014) *Plasmodium falciparum* erythrocyte invasion: combining function with immune invasion. *PloS Pathogens* 10(3), e1003943.

Wright, J., Both, C. *et al.* (1998) Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. *Journal of Animal Ecology* 67, 620–634.

Wright, S. (1931) Evolution in Mendelian populations. *Genetics* 16, 97–159.

Wright, S. (1932) The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proceedings of the 6th International Congress of Genetics* 1, 356–366.

Wright, S. (1975) *Evolution and the Genetics of Populations*. Chicago, Illinois, USA: Chicago University Press.

Wright, S. (1982a) Character change, speciation, and the higher taxa. *Evolution* 36, 427–443.

Wright, S. (1982b) The shifting balance theory and macroevolution. *Annual Review of Genetics* 16, 1–21.

Wu, J-C.., Xu, J-X. *et al.* (2001) Pesticide-induced susceptibility of rice brown planthopper *Nilaparvata lugens*. *Entomologia Experimentalis et Applicata* 100, 119–126.

Wu, J-C., Qiu, H-M. *et al.* (2004) Effective duration of pesticide-induced susceptibility of rice to brown planthopper (*Nilaparvata lugens* (Stål.), Homoptera: Delphacidae), and physiological and biochemical changes in rice plants following pesticide application. *International Journal of Pest Management* 50, 55–62.

Wu, K.M. and Guo, Y.Y. (2005) The evolution of cotton pest management practices in China. *Annual Review of Entomology* 50, 31–52.

Wu, X., Griffin, J.N. *et al.* (2015) The sign of cascading predator effects varies with prey traits in a detrital system. *Journal of Animal Ecology* 84, 1610–1617.

Wynne-Edwards, V.C. (1962) *Animal Dispersion in Relation to Social Behaviour*. Edinburgh, UK: Oliver and Boyd.

Xi, Z., Khoo, C.C.H. *et al.* (2005) *Wolbachia* establishment and invasion in an *Aedes aegypti* population. *Science* 310, 326–328.

Xu, J., De Barro, P.J. *et al.* (2010) Reproductive incompatibility among genetic groups of *Bemisia tabaci* supports the proposition that the whitefly is a cryptic species complex. *Bulletin of Entomological Research* 100, 359–366.

Yakhontov, V.V. (1962) Seasonal migrations of ladybirds *Brumus octosignatus* Gebl. and *Semiadalia unidecimnotata* Schneid. in Central Asia. *Proceedings of the 11th International Congress of Entomology* 3, 21–23.

Yakob, L., Alphey, L. *et al.* (2008) *Aedes aegypti* control: the concomitant roles of competition, space and transgenic technologies. *Journal of Applied Ecology* 45, 1258–1265.

Yamamoto, R.T., Jenkins, R.Y. *et al.* (1969) Factors determining the selection of plants for oviposition by the tobacco hornworm *Manduca sexta*. *Entomologia Experimentalis et Applicata* 12, 504–508.

Yamamura, K. (1999) Key-factor/key stage analysis for life table data. *Ecology* 80, 533–537.

Yamashita, T. and Polis, G.A. (1995) A test of the central-marginal model using sand scorpion populations. *Journal of Arachnology* 23, 60–64.

Yang, Y., Huang, M. *et al.* (2006) Distribution, biology ecology and control of the psyllid *Diaphorina citri* Kuwayama, a major pest of citrus: a status report for China. *International Journal of Pest Management* 52, 343–352.

Yasui, Y. (1997) A “good sperm” model can explain the evolution of costly multiple mating by females. *The American Naturalist* 149, 573–584.

Yocum, G.D., Rinehart, J.P. *et al.* (2012) Water balance in the sugarbeet root maggot *Tetanops myopaeformis*, during long term low temperature storage and after freezing. *Physiological Entomology* 37, 340–344.

Yovanovitch, P. (1888) *Entomologie Appliquée a la Medicine Légale*. Paris, France: Ollier-Henrey.

Yu, D.S., Luck, R.F. *et al.* (1990) Competition, resource partitioning and coexistence of an endoparasitoid *Encarsia perniciosi* and an ectoparasitoid *Aphytis melinus* of the California red scale. *Ecological Entomology* 15, 469–480.

Yukawa, J., Miyamoto, K. *et al.* (2016) Key-factor/key stage analysis of long-term life table data for a fruit gall midge, *Asphondylia sphaera* (Diptera: Cecidomyiidae). *Ecological Entomology* 41, 516–526.

Zaady, E. and Shachak, M. (1994) Microphytic soil crust and ecosystem leakage in the Negev Desert. *American Journal of Botany* 81, 109.

Zachariassen, K.E. (1991) The water relations of overwintering insects. In: Lee, R.E. and Denlinger, D.L. (eds) *Insects at Low Temperature*. New York, New York, USA: Chapman and Hall, pp. 47–63.

Zaim, M. and Newson, H.D. (1980) Effect of waste water spray irrigation on indigenous mosquito populations. *Environmental Entomology* 9, 563–566.

Zang, L-S. and Liu, T-X. (2008) Host-feeding of three parasitoid species on *Bemisia tabaci* biotype B and implications for whitefly biological control. *Entomologia Experimentalis et Applicata* 127, 55–63.

Zelazny, B. and Alfiler, A.R. (1991) Ecology of baculovirus-infected and healthy adults of *Oryctes rhinoceros* (Coleoptera: Scarabaeidae) on coconut palms in the Philippines. *Ecological Entomology* 16, 253–259.

Zera, A.J. and Denno, R.F. (1997) Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Entomology* 42, 207–231.

Zera, A.J. and Harshman, L.G. (2001) The physiology of life-history trade-offs in animals. *Annual Review of Ecology and Systematics* 32, 95–126.

Zetto Brandmayr, T. (1990) Spermatophagous (seed-eating) ground beetles: first comparison of the diet of the harpaline genera *Harpalus* and *Ophonus* (Col., Carabidae). In: Stork, N.E. (ed.) *The Role of Ground Beetles in Ecological and Environmental Studies*. Andover, UK: Intercept.

Zhang, C-L., Xu, D-C. *et al*. (2008) Genetic approaches to sustainable pest management in sugar beet (*Beta vulgaris*). *Annals of Applied Biology* 152, 143–156.

Zhang, Q-B. and Alfaro, R.I. (2003) Spatial synchrony of the two-year cycle budworm outbreaks in central British Columbia, Canada. *Oikos* 103, 146–154.

Zhang, Z., Cazelles, B. *et al*. (2009) Periodic temperature-associated drought/flood drives locust plagues in China. *Proceedings of the Royal Society B* 276, 823–831.

Zhao, W-C., Cheng, J-A. *et al*. (2004) Development of a monoclonal antibody to detect predation of the brown planthopper *Nilaparvata lugens* (Stål). *International Journal of Pest Management* 50, 317–321.

Zhou, G., Overholt, W.A. *et al*. (2003) Species richness and parasitism in an assemblage of parasitoids attacking maize stem borers in coastal Kenya. *Ecological Entomology* 28, 109–118.

Zhou, Z-S., Rasmann, S. *et al*. (2015) mating frequency positively associates with fitness in *Ophraella communa*. *Ecological Entomology* 40, 292–298.

Zhu, F., Lammers, M. *et al*. (2016) Intrinsic competition between primary hyperparasitoids of the solitary parasitoid *Cotesia rubecula*. *Ecological Entomology* 41, 292–300.

Ziegler, R. and Schulz, M. (1986a) Regulation of lipid metabolism during flight in *Manduca sexta*. *Journal of Insect Physiology* 32, 903–908.

Ziegler, R. and Schulz, M. (1986b) Regulation of carbohydrate metabolism during flight in *Manduca sexta*. *Journal of Insect Physiology* 32, 997–1001.

Zimmer, C. (1999) Life after chaos. *Science* 284, 83–86.

Zimmermann, K., Fric, Z. *et al*. (2011) Mark-recapture on a large spatial scale reveals long-distance dispersal in the marsh fritillary, *Euphydryas aurinia*. *Ecological Entomology* 36, 499–510.

Zucker, W.V. (1983) Tannins: does structure determine function? An ecological perspective. *The American Naturalist* 121, 335–365.

Zuk, M. (1987) The effect of gregarine parasites on longevity, weight loss and developmental time in the field crickets *Gryllus veletis* and *G. pennsylvanicus*. *Ecological Entomology* 12, 349–354.

Zuk, M. and Kolluru, G.R. (1998) Exploitation of sexual signals by predators and parasitoids. *The Quarterly Review of Biology* 73, 415–438.

Zumpt, F. (1965) *Myiasis in Man and Animals in the Old World. A Textbook for Physicians, Veterinarians and Zoologists*. London, UK: Butterworth.

Zvereva, E.L. and Rank, N.E. (2003) Host plant effects on parasitoid attack on the leaf beetle *Chrysomela lapponica*. *Oecologia* 135, 258–267.

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Ecological and Economic Entomology

A Global Synthesis

B. E. Freeman

Ecological and Economic Entomology is a comprehensive advanced text covering all aspects of the role of insects in natural ecosystems and their impacts on human activity.

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