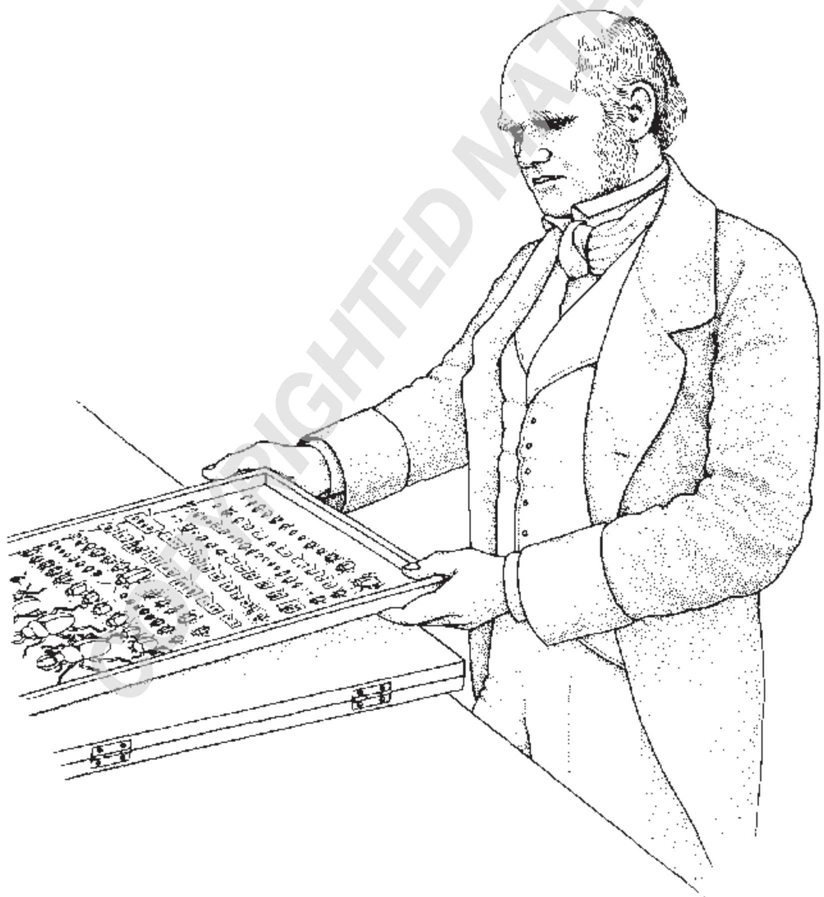
Chapter 1

THE IMPORTANCE, DIVERSITY AND CONSERVATION OF INSECTS



Charles Darwin inspecting beetles collected during the voyage of the *Beagle*. (After various sources, especially Huxley & Kettlewell 1965 and Futuyma 1986.)

Curiosity alone as to the identities and lifestyles of the fellow inhabitants of our planet justifies the study of insects. Some of us have used insects as totems and symbols in spiritual life, and we portray them in art and music. If we consider economic factors, the effects of insects are enormous. Few human societies lack honey, which is provided by bees (or specialized ants). Insects pollinate our crops. Many insects share our houses, agriculture and food stores. Others live on us, on our domestic pets or our livestock, and more visit to feed on us, where they may transmit disease. Clearly, we should understand these pervasive animals.

Although there are millions of kinds of insects, we do not know exactly (or even approximately) how many. This ignorance as to how many organisms we share our planet with is remarkable considering that astronomers have listed, mapped and uniquely identified a comparable diversity of galactic objects. Some estimates, which we discuss in detail later, imply that the species richness of insects is so great that, to a near approximation, all organisms can be considered to be insects. Although dominant on land and in freshwater, few insects are found beyond the tidal limit of oceans.

In this opening chapter, we outline the significance of insects and discuss their diversity and classification, and their roles in our economic and wider lives. First, we outline the field of entomology and the role of entomologists, and then introduce the ecological functions of insects. Next, we explore insect diversity, and then discuss how we name and classify this immense diversity. Sections follow in which we consider some cultural and economic aspects of insects, their aesthetic and tourism appeal, their conservation, and how and why they may be reared. We conclude with a section on insects as food for humans and animals. In text boxes we discuss citizen involvement in entomology (Box 1.1), the phenomenal growth of butterfly houses (Box 1.2), the effects of tramp ants on biodiversity (Box. 1.3), the conservation of the large blue butterfly in England (Box 1.4) and insect threats to palm trees (Box 1.5).

1.1 WHAT IS ENTOMOLOGY?

Entomology is the study of insects. Entomologists are the people who study insects, and observe, collect, rear and experiment with insects. Research undertaken by entomologists covers the total range of biological disciplines, including evolution, ecology, behaviour, anatomy, physiology, biochemistry and genetics. The unifying feature is that the study organisms are insects. Biologists work with insects for many reasons: ease of culturing in a laboratory, rapid population turnover, and availability of many individuals are important factors. The minimal ethical concerns regarding responsible experimental use of insects, as compared with vertebrates, are a significant consideration.

Modern entomological study commenced in the early 18th century when a combination of rediscovery of the classical literature, the spread of rationalism, and the availability of ground-glass optics made the study of insects acceptable for the thoughtful privately wealthy. Although today many people working with insects hold professional positions, some aspects remain suitable for informed citizens (Box 1.1). Charles Darwin's initial enthusiasm in natural history was as a collector of beetles (as shown in the vignette for this chapter) and throughout his life he communicated with amateur entomologists throughout the world. Much of our present understanding of worldwide insect diversity is derived from studies of non-professionals. Many such contributions come from collectors of attractive insects such as butterflies and beetles, but others with patience and ingenuity continue the tradition of Jean-Henri Fabre in observing close-up the activities of insects. We can discover much of scientific interest at little expense regarding the natural history of even "well-known" insects. The variety of size, structure and colour in insects (see **Plate 1a–f**) is striking, whether depicted in drawings, photographs or movies.

A popular misperception is that professional entomologists emphasize killing or controlling insects, but numerous entomological studies document their beneficial roles.

1.2 THE IMPORTANCE OF INSECTS

There are many reasons why we should study insects. Their ecologies are incredibly variable. Insects may dominate food chains and food webs in terms of both

The Insects: An Outline of Entomology, Fifth Edition. P.J. Gullan and P.S. Cranston.

Companion Website: www.wiley.com/go/gullan/insects

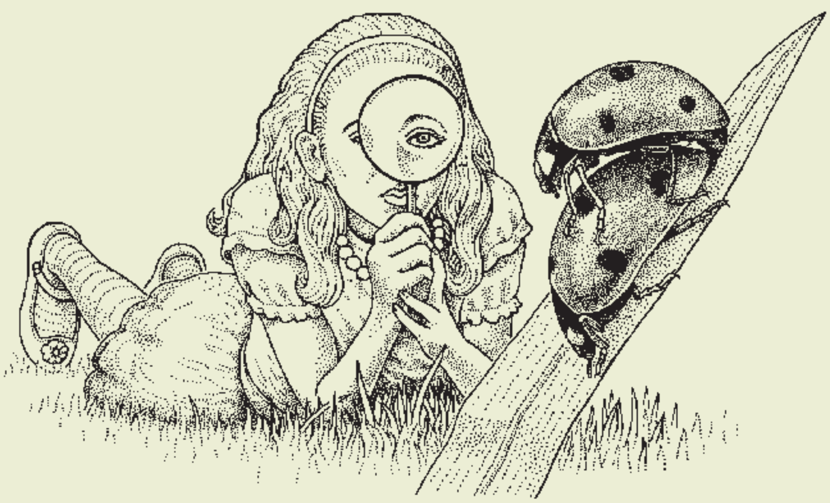
Box 1.1 Citizen entomologists – community participation

The involvement of non-professional "citizen scientists" in biodiversity studies dates back at least to the 18th century, especially in the United Kingdom. Published guides to the fauna became best-sellers – Victorian ladies of leisure studied the flora and collected shells and fossils, wealthy gentlemen shot rare birds and collected their eggs, and the rich assembled "cabinets of curios" that became the world-renowned natural history collections of the great museums. Darwin, portrayed in the vignette at the beginning of this chapter, was a skilled collector and student of the Coleoptera, and many church curates, with little to do between Sunday sermons, were serious entomologists at a time when few were paid for such studies.

Despite the transformation of natural history into a professional science, areas such as floristics and ornithology continue to benefit from amateur involvement. The ever-increasing availability of internet-based guides to images, distribution maps, bird-songs, etc., encourages involvement of citizens in recording many facets of the biota of their local areas. The more popular insects are also subjects of interest to a wider public, and there is substantial participation in reporting occurrences, particularly for butterflies, dragonflies, wasps and bees, and beetles. Especially in Europe and North America, many can be identified (some more easily than others) without killing the insect, by eye or by using a hand lens. With digital photography, excellent macro-images can be passed to experts for confirmation of identification, used to "voucher" observations, and validated records then can be entered into databases. Citizen-collected records are valuable in establishing distributions and temporal presence (e.g. early and late dates for appearance) – and have assisted in documentation for conservation and for assessing effects of climate change.

The longest lasting, and surely largest, participatory survey, the Rothamsted Insect Survey, has used light-traps at over 430 sites in the United Kingdom, many operated by volunteers, since the 1960s. More than 730 species of macrolepidoptera have been recognized since the survey began, and more than 10 million data points (species identity × location × date × abundance) have been databased. Although this resource is used widely to infer effects of climate change, most studies infer that observed declines in lepidopteran populations relate more to the staggering loss of natural habitats to agriculture, with climate effects evident most in the previous years' summer conditions.

In the United States, citizen scientists have been recruited to collect long-term data on sightings of migrating butterflies, eggs and larval populations of the monarch butterfly (*Danaus plexippus*) and its milkweed habitat. Volunteers contribute to monarch conservation by regular monitoring of their local sites. One major goal is to understand how and why monarch populations vary in time and space, particularly during the breeding season in North America.



The United Kingdom's Ladybird Survey provides another example of public participation in insect recording. Ladybirds (called lady beetles or ladybugs in the United States; a pair of copulating adults is illustrated here) are common, colourful, and can be identified with appropriate guidance (using a "Ladybird Atlas") built on several pre-existing specialist recording schemes. A website (http://www.ladybird-survey.org/) provides much information to help find and identify species, and provides online forms to record observations. There is great value in this scheme, as evidenced by the recent invasion of the United Kingdom by the East Asian harlequin ladybird (*Harmonia axyridis*); documentation of its spread and the impact on native ladybirds has been possible due to existing community surveys. Such a project requires a good existing database: the impacts of this introduced species in the United States can only be surmised as pre-invasion data are inadequate.

Global recording of odonates (dragonflies and damselflies) by amateurs is very popular, especially in Asia. As with small birds, identifications can be made at some distance using binoculars (as illustrated here). Photographic vouchers can be taken while the insects are sedentary (e.g. at dawn). Care must be taken though not to assume that the presence of adult odonates indicates water conditions suitable for nymphal development since adults are strong flyers (see section 10.5 on biomonitoring).

As with all observational data, appropriate checks on identifications are important and observer biases often occur. Thus citizen-science data should be interpreted with caution, although there is little doubt as to the value of data collection by an interested and informed public.

volume and numbers. Feeding specializations of different insect groups include ingestion of detritus, rotting materials, wood and fungus (Chapter 9), aquatic filter feeding and grazing (Chapter 10), herbivory (= phytophagy), including sap feeding (Chapter 11), and predation and parasitism (Chapter 13). Insects may live in water, on land, or in soil, during part or all of their lives. Their lifestyles may be solitary, gregarious, subsocial or highly social (Chapter 12). They may be conspicuous, mimics of other objects, or concealed (Chapter 14), and may be active by day or by night. Insect life cycles (Chapter 6) allow survival under a wide range of conditions, such as extremes of heat and cold, wet and dry, and unpredictable climates.

Insects are essential to the following ecosystem functions:

- nutrient recycling, via leaf-litter and wood degradation, dispersal of fungi, disposal of carrion and dung, and soil turnover;
- plant propagation, including pollination and seed dispersal;
- maintenance of plant community composition and structure, via phytophagy, including seed feeding;

• food for insectivorous vertebrates, such as many birds, mammals, reptiles and fish;
• maintenance of animal community structure, through transmission of diseases of large animals, and predation and paratization of smaller ones.

Each insect species is part of a greater assemblage and its loss affects the complexities and abundance of other organisms. Some insects are considered "**keystone species**" because loss of their critical ecological functions could lead to collapse of the wider ecosystem. For example, termites convert cellulose in tropical soils (section 9.1), suggesting that they are keystones in tropical soil structuring. In aquatic ecosystems, a comparable service is provided by the guild of mostly larval insects that breaks down and releases the nutrients from wood and leaves derived from the surrounding terrestrial environment.

Insects are associated intimately with our survival, in that certain insects damage our health and that of our domestic animals (Chapter 15) and others adversely affect our agriculture and horticulture (Chapter 16). Certain insects greatly benefit human society, either by providing us with food directly or by contributing to our food or materials that we use. For example, honey bees not only provide us with honey but also are valuable agricultural pollinators worth an additional estimated US$15 billion annually in increased crop yields in the United States alone. Also the quality of bee-pollinated fruits can exceed that of fruits pollinated by wind or selfing (see section 11.3.1). Furthermore, estimates of the value of pollination by wild, free-living bees is US$1.0–2.4 billion per year for California alone. The total economic value of pollination services estimated for the 100 crops used directly for human food globally exceeds US$200 billion annually. Furthermore, valuable services, such as those provided by predatory beetles and bugs or parasitic wasps that control pests, often go unrecognized, especially by city-dwellers, and yet such ecosystem services are worth billions of US$ annually.

Insects contain a vast array of chemical compounds, some of which can be collected, extracted or synthesized for our use. Chitin, a component of insect cuticle, and its derivatives act as anticoagulants, enhance wound and burn healing, reduce serum cholesterol, serve as non-allergenic drug carriers, provide strong biodegradable plastics, and enhance removal of pollutants from waste water, to mention just a few developing applications. Silks from the cocoons of silkworm moths, *Bombyx mori*, and related species have been used for fabric for centuries, and two endemic South African species may be increasing in local value. The red dye cochineal is obtained commercially from scale insects of *Dactylopius coccus* cultured on *Opuntia* cacti. Another scale insect, the lac insect *Kerria lacca*, is a source of a commercial varnish called shellac. Given this range of insect-produced chemicals, and accepting our ignorance of most insects, there is a high likelihood that novel chemicals await our discovery and use.

Insects provide more than economic or environmental benefits; characteristics of certain insects make them useful models for understanding general biological processes. For instance, the short generation time, high fecundity, and ease of laboratory rearing and manipulation of the vinegar or common fruit fly, *Drosophila melanogaster*, have made it a model research organism. Studies of *D. melanogaster* have provided the foundations for our understanding of genetics and cytology, and these flies continue to provide the experimental materials for advances in molecular biology, embryology and development. Outside the laboratories of geneticists, studies of social insects, notably hymenopterans such as ants and bees, have allowed us to understand the evolution and maintenance of social behaviours such as altruism (section 12.4.1). The field of sociobiology owes its existence to entomologists' studies of social insects. Several theoretical ideas in ecology have derived from the study of insects. For example, our ability to manipulate the food supply (cereal grains) and number of individuals of flour beetles (*Tribolium* spp.) in culture, combined with their short life history (compared to most vertebrates), has provided insights into how populations are regulated. Some concepts in ecology, for example the ecosystem and niche, came from scientists studying freshwater systems where insects dominate. Alfred Wallace (depicted in the vignette of Chapter 18), the independent and contemporaneous discoverer with Charles Darwin of the theory of evolution by natural selection, based his ideas on observations of tropical insects. Hypotheses concerning the many forms of mimicry and sexual selection derive from observations of insect behaviour, which continue to be investigated by entomologists.

Finally, the sheer numbers of insects means that their impact upon the environment, and hence our lives, is highly significant. Insects are the major component of macroscopic biodiversity and, for this reason alone, we should try to understand them better.

1.3 INSECT BIODIVERSITY

1.3.1 The described taxonomic richness of insects

Probably slightly over one million species of insects have been described, that is, have been recorded in a taxonomic publication as "new" (to science that is), accompanied by a description and often with illustrations or some other means of recognizing the particular insect species (section 1.4). Since some insect species have been described as new more than once, due to failure to recognize variation or through ignorance of previous studies, the actual number of described species is uncertain.

The described species of insects are distributed unevenly amongst the higher taxonomic groupings called orders (section 1.4). Five "major" orders stand out for their high species richness: the beetles (Coleoptera); flies (Diptera); wasps, ants and bees (Hymenoptera); butterflies and moths (Lepidoptera); and the true bugs (Hemiptera). J.B.S. Haldane's jest – that "God" (evolution) shows an inordinate "fondness" for beetles – appears to be confirmed since they comprise almost 40% of described insects (more than 350,000 species). The Hymenoptera have more than 150,000 described species, with the Diptera and Lepidoptera having at least 150,000 described species each, and Hemiptera over 100,000. Of the remaining orders of living insects, none exceed the approximately 24,000 described species of the Orthoptera (grasshoppers, locusts, crickets and katydids). Most of the "minor" orders comprise some hundreds to a few thousands of described species. Although an order may be described as "minor", this does not mean that it is insignificant – the familiar earwig belongs to an order (Dermaptera) with fewer than 2000 described species, and the ubiquitous cockroaches belong to an order (Blattodea, which includes termites) with only about 7500 species. Moreover, there are only twice as many species described in Aves (birds) as in the "small" order Blattodea.

1.3.2 The estimated taxonomic richness of insects

Surprisingly, the figures given above, which represent the cumulative effort by many insect taxonomists from all parts of the world over some 250 years, appear to represent something less than the true species richness of the insects. Just how far short is the subject of continuing speculation. Given the very high numbers and the patchy distributions of many insects in time and space, it is impossible in our time-scales to inventory (count and document) all species even for a small area. Extrapolations are required to estimate total species richness, which range from some three million to as many as 80 million species. These various calculations either extrapolate ratios for richness in one taxonomic group (or area) to another unrelated group (or area), or use a hierarchical scaling ratio, extrapolated from a subgroup (or subordinate area) to a more inclusive group (or wider area).

Generally, ratios derived from temperate/tropical species numbers for well-known groups such as vertebrates provide rather conservatively low estimates if used to extrapolate from temperate insect taxa to essentially unknown tropical insect faunas. The most controversial estimation, based on hierarchical scaling and providing the highest estimated total species numbers, was an extrapolation from samples from a single tree species to global rainforest insect species richness. Sampling used insecticidal fog to assess the little-known fauna of the upper layers (the canopy) of Neotropical rainforest. Much of this estimated increase in species richness was derived from arboreal beetles (Coleoptera), but several other canopy-dwelling groups were found to be much more numerous than believed previously. Key factors in calculating tropical diversity included identification of the number of beetle species found, estimation of the proportion of novel (previously unseen) groups, estimation of the degree of host-specificity to the surveyed tree species, and the ratio of beetles to other arthropods. Certain assumptions have been tested and found to be suspect, notably, host-plant specificity of herbivorous insects, at least in some tropical forests, seems very much less than estimated early on in this debate.

Estimates of global insect diversity calculated from experts' assessments of the proportion of undescribed versus described species amongst their study insects tend to be comparatively low. Belief in lower numbers of total species comes from our general inability to confirm the prediction, which is a logical consequence of the high species-richness estimates, that insect samples ought to contain very high proportions of previously unrecognized and/or undescribed ("novel") taxa. Obviously, any expectation of an even spread of novel species is unrealistic, since some groups and regions of the world are poorly known compared to others. However, amongst the minor (less species-rich) orders there is little or no scope for dramatically increased, unrecognized species richness. Very high levels of novelty, if they do exist, realistically could only be amongst the Coleoptera, Diptera, Lepidoptera and parasitic Hymenoptera. Molecular techniques, for example **DNA barcoding**, sometimes in conjunction with trained biodiversity technicians (**parataxonomists**), reveal high levels of cryptic (hidden) diversity of the latter two groups in Costa Rica (see Box 7.3).

Nevertheless, some (but not all) recent re-analyses tend towards the lower end of the range of estimates derived from taxonomists' calculations and extrapolations from regional sampling rather than those derived from ecological scaling. A figure of between two and six million species of insects appears realistic.

1.3.3 The location of insect species richness

The regions in which additional undescribed insect species might occur (i.e. up to an order of magnitude greater number of novel species than described) cannot be in the northern hemisphere, where such hidden diversity in the well-studied faunas is unlikely. For example, the British Isles inventory of about 22,500 species of insect is likely to be within 5% of being complete, and the 30,000 or so described from Canada must represent over half of the total species. Any hidden diversity is not in the Arctic, with some 3000 species present in the American Arctic, nor in Antarctica, the southern polar mass, which supports a bare handful of insects. Evidently, just as species-richness patterns are uneven across groups, so too is their geographic distribution.

Despite the lack of necessary local species inventories to prove it, tropical species richness appears to be much higher than that of temperate areas. For example, a single tree surveyed in Peru produced 26 genera and 43 species of ants: a tally that equals the total ant diversity from all habitats in Britain. Our inability to be certain about finer details of geographical patterns stems in part from entomologists interested in biodiversity issues being based mostly in the temperate northern hemisphere, whereas the centres of richness of the insects themselves are in the tropics and southern hemisphere.

Studies in tropical American rainforests suggest that much undescribed novelty in insects does come from the beetles, which provided the basis for the original high species-richness estimate. Although beetle dominance may be true in places such as the Neotropics, this might be an artefact of research biases of entomologists. In some well-studied temperate regions such as the United Kingdom and Canada, species of true flies (Diptera) appear to outnumber beetles. Studies of canopy insects on the tropical island of Borneo have shown that both Hymenoptera and Diptera can be more species rich at particular sites than the Coleoptera. Comprehensive regional inventories or credible estimates of insect faunal diversity may eventually tell us which order of insects is globally most diverse.

Whether we estimate 30–80 million species or an order of magnitude less, insects constitute at least half of global species diversity (Fig. 1.1). If we consider only life on land, insects comprise an even greater proportion of extant species, since the radiation of insects is a predominantly terrestrial phenomenon. The relative contribution of insects to global diversity will be somewhat lessened if marine diversity, to which insects make a negligible contribution, actually is higher than currently understood.

1.3.4 Some reasons for insect species richness

Whatever the global estimate is, insects surely are remarkably speciose. This high species richness has been attributed to several factors. The small size of insects, a limitation imposed by their method of gas

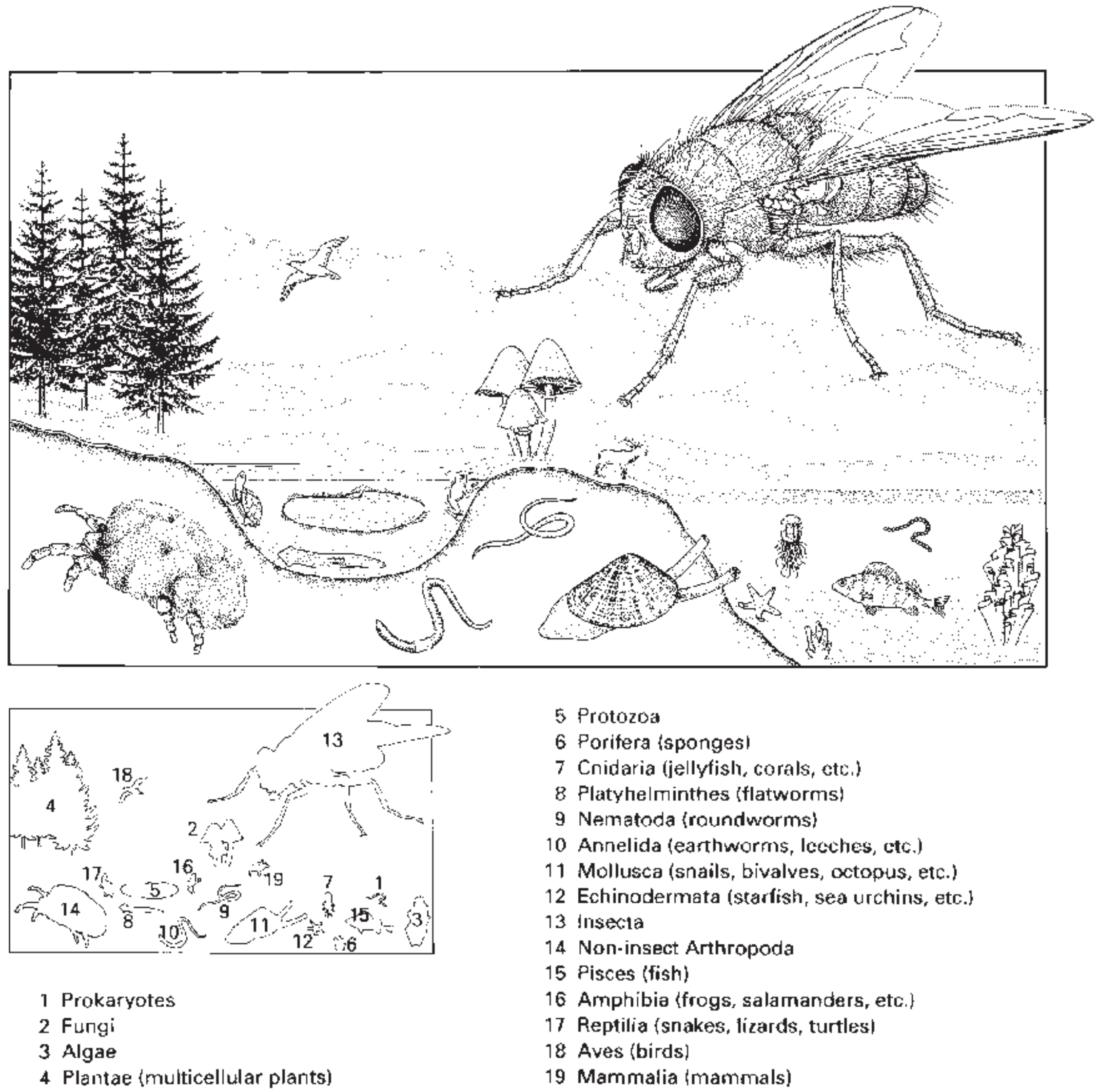


Fig. 1.1 Speciescape, in which the size of individual organisms is approximately proportional to the number of described species in the higher taxon that it represents. (After Wheeler 1990.)

exchange via tracheae, is an important determinant. Many more niches exist in any given environment for small organisms than for large organisms. Thus, a single acacia tree, that feeds one giraffe, supports the complete life cycle of dozens of insect species: a lycaenid butterfly larva chews the leaves; a bug sucks the stem sap; a longicorn beetle bores into the wood; a midge galls the flower buds; a bruchid beetle destroys the seeds; a mealybug sucks the root sap; and several wasp species parasitize each host-specific phytophage. An adjacent acacia of a different species feeds the same giraffe but may have a very different suite of phytophagous insects. The environment is more fine-grained from an insect's perspective compared to that of a mammal or bird.

Small size alone is insufficient to allow exploitation of this environmental heterogeneity, since organisms must be capable of recognizing and responding to environmental differences. Insects have highly organized sensory and neuromotor systems, which are more comparable to those of vertebrate animals than to those of other invertebrates. However, insects differ from vertebrates both in size and in how they respond to environmental change. Generally, vertebrate animals are longer lived than insects and individuals can adapt to change by some degree of learning. Insects, on the other hand, normally respond to, or cope with, altered conditions (e.g. the application of insecticides to their host plant) by genetic change between generations (e.g. leading to insecticide resistant insects). High genetic heterogeneity or elasticity within insect species allows persistence in the face of environmental change. Persistence exposes species to processes that promote speciation, predominantly involving phases of range expansion and/or subsequent fragmentation. Stochastic processes (genetic drift) and/or selection pressures provide the genetic alterations that may become fixed in spatially or temporally isolated populations.

Insects possess characteristics that expose them to other potentially diversifying influences that enhance their species richness. Interactions between certain groups of insects and other organisms, such as plants in the case of herbivorous insects, or hosts for parasitic insects, may promote the genetic diversification of eater and eaten (section 8.6). These interactions are often called coevolutionary and are discussed in more detail in Chapters 11 and 13. The reciprocal nature of such interactions may speed up evolutionary change in one or both partners or sets of partners, perhaps even leading to major radiations in certain groups. Such a scenario involves increasing specialization of insects, at least on plant hosts. Evidence from phylogenetic studies suggests that this has happened – but also that generalists may arise from within a specialist radiation, perhaps after some plant chemical barrier has been overcome. Waves of specialization followed by breakthrough and radiation must have been a major factor in promoting the high species richness of phytophagous insects.

Another explanation for the high species numbers of insects is the role of sexual selection in the diversification of many insects. The propensity of insects to become isolated in small populations (because of the fine scale of their activities) in combination with sexual selection (sections 5.3 and 8.6) may lead to rapid alteration in intra-specific communication. When (or if) the isolated population rejoins the larger parental population, altered sexual signalling deters hybridization and the identity of each population (incipient species) is maintained despite the sympatry. This mechanism is seen to be much more rapid than genetic drift or other forms of selection, and need involve little if any differentiation in terms of ecology or non-sexual morphology and behaviour.

Comparisons among insect groups and between insects and their close relatives may suggest some reasons for insect diversity. Which characteristics are shared by the most speciose insect orders: the Coleoptera, Hymenoptera, Diptera and Lepidoptera? Which features of insects do other arthropods, such as arachnids (spiders, mites, scorpions and their allies) lack? No simple explanation emerges from such comparisons; probably design features, flexible life-cycle patterns and feeding habits play a part (some factors are explored in Chapter 8). In contrast to the most speciose insect groups, arachnids lack winged flight, lack complete transformation of body form during development (metamorphosis) and lack dependence on specific food organisms, and generally do not feed on plants. Exceptionally, mites, the most diverse and abundant of arachnids, have many very specific associations with other living organisms, including with plants.

High persistence of species or lineages, or the numerical abundance of individual species are considered as indicators of insect success. However, insects differ from vertebrates by at least one popular measure of success: body size. Miniaturization is the insect success story: most insects have body lengths of 1–10 mm, with a body length of around 0.3 mm in mymarid wasps (which are parasitic on eggs of insects) being unexceptional. At the other extreme, the greatest wingspan in a living insect belongs to the tropical American owlet moth, *Thysania agrippina* (Noctuidae), with a span of up to 30 cm, although fossils show that some extinct insects were appreciably larger than their living relatives. For example, an Upper Carboniferous silverfish, *Ramsdelepidion schusteri* (Zygentoma), had a body length of 6 cm, as compared to a modern maximum of less than 2 cm. The wingspans of many Carboniferous insects exceeded 45 cm, and a Permian dragonfly, *Meganeuropsis americana* (Meganisoptera), had a wingspan of 71 cm. Notably, amongst these large insects, the great size is predominantly associated with a narrow, elongate body, although one of the heaviest extant insects, the Hercules beetle, *Dynastes hercules* (Scarabaeidae), with a body up 17 cm long, is an exception in having a bulky body. The heaviest recorded insect is a weta (Anostostomatidae; see **Plate 1d**), with a female of the bulky Little Barrier Island giant weta, *Deinacrida heteracantha,* weighing 71 g.

Barriers to large size include the inability of the tracheal system to diffuse gases across extended distances from active muscles to and from the external environment (see Box 3.2). Further elaborations of the tracheal system would jeopardize water balance in a large insect. Most large insects are narrow and have not greatly extended the maximum distance between the external oxygen source and the muscular site of gaseous exchange, compared with smaller insects. A possible explanation for the gigantism of some Palaeozoic insects is considered in Box 8.2.

In summary, many insect radiations probably depended upon: (i) the small size of individuals, combined with (ii) short generation time, (iii) sensory and neuromotor sophistication, (iv) evolutionary interactions with plants and other organisms, (v) metamorphosis, and (vi) mobile winged adults. The substantial time since the origin of each major insect group has allowed many opportunities for lineage diversification (Chapter 8). Present-day species diversity results from either higher rates of speciation (for which there is limited evidence) and/or lower rates of species extinction (higher persistence) than other organisms. The high species richness seen in some (but not all) groups in the tropics may result from the combination of higher rates of species formation with high species accumulation in equable climates.

1.4 NAMING AND CLASSIFICATION OF INSECTS

The formal naming of insects follows the rules of nomenclature developed for all animals (plants have a slightly different system). Formal scientific names are required for unambiguous communication between all scientists, no matter what their native language. Vernacular (common) names do not fulfil this need: the same insects may even have different vernacular names amongst people who speak the same language. For instance, the British refer to "ladybirds", whereas the same coccinellid beetles are "ladybugs" to many people in the United States. Many insects have no vernacular name, or a common name is given to multiple species as if only one species is involved. These difficulties are addressed by the Linnaean system, which provides every described species with two given names (the binomen). The first is the generic (genus) name, used for a broader grouping than the second name, which is the specific (species) name. These Latinized names always are used together and are italicized, as in this book. The combination of genus and species names provides each organism with a unique name. Thus, the name *Aedes aegypti* is recognized by any medical entomologist, anywhere, whatever the local name (and there are many) for this disease-transmitting mosquito. Ideally, all taxa should have such a Latinized binomen, but in practice some alternatives may be used prior to naming formally (section 18.3.2).

In scientific publications, the species name often is followed by the name of the original describer of the species and perhaps the year in which the name first was published legally. In this book, we do not follow this practice but, in discussion of particular insects, we give the order and family names to which the species belongs. In publications, after the first citation of the combination of genus and species names in the text, it is common practice in subsequent citations to abbreviate the genus to the initial letter only (e.g. *A. aegypti*). However, where this might be ambiguous, such as for the two mosquito genera *Aedes* and *Anopheles*, the initial two letters *Ae.* and *An.* are used, as in Chapter 15.

Various taxonomically defined groups, also called taxa (singular: **taxon**), are recognized amongst the insects. As for all other organisms, the basic biological taxon, lying above the individual and population, is the species, which is both the fundamental nomenclatural unit in taxonomy and, arguably, a unit of evolution. Multi-species studies allow recognition of genera, which are discrete higher groups. In a similar manner, genera can be grouped into tribes, tribes into subfamilies, and subfamilies into families. The families of insects are placed in relatively large but easily recognized groups called orders. This hierarchy of ranks (or categories) thus extends from the species

Table 1.1 Taxonomic categories (obligatory categories are shown in **bold**).

Taxon category	Standard suffix	Example
Order		Hymenoptera
Suborder		Apocrita
Superfamily	-oidea	Apoidea
Epifamily	-oidae	Apoidae
Family	-idae	Apidae
Subfamily	-inae	Apinae
Tribe	-ini	Apini
Genus		*Apis*
Subgenus		
Species		*A. mellifera*
Subspecies		*A. m. mellifera*

level through a series of "higher" levels of greater and greater inclusivity until all true insects are included in one class, the Insecta. There are standard suffixes for certain ranks in the taxonomic hierarchy, so that the rank of most group names can be recognized by inspection of the ending (Table 1.1).

Depending on the classification system used, some 25 to 30 orders of Insecta may be recognized. Differences arise principally because there are no fixed rules for deciding the taxonomic ranks referred to above – only general agreement that groups should be monophyletic, comprising all the descendants of a common ancestor (section 7.1.1). Over time, a relatively stable classification system has developed, but differences of opinion remain as to the boundaries around and among groups, with "splitters" recognizing a greater number of groups and "lumpers" favouring broader categories. For example, some North American taxonomists group ("lump") the alderflies, dobsonflies, snakeflies and lacewings into one order, the Neuroptera, whereas others, including ourselves, "split" the group and recognize three separate (but clearly closely related) orders, Megaloptera, Raphidioptera, and a more narrowly defined Neuroptera (see Fig. 7.2). The order Hemiptera has sometimes been divided into two orders, Homoptera and Heteroptera, but the homopteran grouping is invalid (non-monophyletic) and we advocate a different classification for these bugs as shown in Fig. 7.6 and discussed in section 7.4.2 and Taxobox 20. New data and methods of analysis are further causes of instability in the recognition of insect orders. As we show in Chapter 7, two groups (termites and parasitic lice) previously treated as orders, belong within each of two other orders and thus the ordinal count is reduced by two.

We recognize 28 orders of insects, with relationships considered in section 7.4 and the physical characteristics and biologies of their constituent taxa described in taxoboxes near the end of the book. A summary of the diagnostic features of all orders and a few subgroups, plus cross references to fuller identificatory and ecological information, appear in tabular form in the reference guide to orders in the Appendix at the end of the book.

1.5 INSECTS IN POPULAR CULTURE AND COMMERCE

People have been attracted to the beauty or mystique of certain insects throughout history. We know the importance of scarab beetles to the Egyptians as religious items, and earlier shamanistic cultures elsewhere in the Old World made ornaments that represent scarabs and other beetles including buprestids (jewel beetles). In Old Egypt the scarab, which shapes dung into balls, is identified as a potter; similar insect symbolism extends also further east. Egyptians, and subsequently the Greeks, made ornamental scarabs from many materials including lapis lazuli, basalt, limestone, turquoise, ivory, resins, and even valuable gold and silver. Such adulation may have been the pinnacle that an insect lacking economic importance ever gained in popular and religious culture, although many human societies recognized insects in their ceremonial lives. The ancient Chinese regarded cicadas as symbolizing rebirth or immortality. In Mesopotamian literature the *Poem of Gilgamesh* alludes to odonates (dragonflies/damselflies) as signifying the impossibility of immortality. In martial arts the swaying and sudden lunges of a praying mantis are evoked in Chinese praying mantis kung fu. The praying mantis carries much cultural symbolism, including creation and patience in zen-like waiting for the San ("bushmen") of the Kalahari. Honeypot ants *(yarumpa)* and witchety grubs (*udnirringitta*) figure amongst the personal or clan totems of Aboriginal Australians of the Arrernte language groups. Although important as food in the arid central Australian environment (see section 1.8.1), these insects were not to be eaten by clan members belonging to that particular totem.

Totemic and food insects are represented in many Aboriginal artworks in which they are associated with cultural ceremonies and the depiction of important locations. Insects have had a place in many societies for their symbolism – such as ants and bees representing hard workers throughout the Middle Ages of Europe, where they even entered heraldry. Crickets, grasshoppers, cicadas, and scarab and lucanid beetles have long been valued as caged pets in Japan. Ancient Mexicans observed butterflies in detail, and lepidopterans were

Box 1.2 Butterfly houses

It used to be that seeing tropical butterflies entailed an expensive visit to an exotic location in order to appreciate their living diversity of shape and colours. Now many children are not far from a tropical butterfly house displaying, for a quite modest entry fee, many examples of some of the showiest lepidopterans. These live insects fly free in spacious walk-in cages or greenhouses replete with tropical vegetation and the appropriate mood sounds of a remote rainforest.

In just 35 years, the number of butterfly houses worldwide has gone from none to several hundred, attracting an estimated 40 million annual visitors and with a global turnover valued at some US$100 million. Equally dramatic has been the conversion from networks of local suppliers to industrial-scale insect production facilities. Although an estimated 4000 species of butterflies have been reared in the tropics, for the past decade some 500 have been listed for sale, and worldwide a core of only 50 species constitute most of those traded, primarily as live pupae. Papilionidae, including the well-known swallowtails, graphiums and birdwings, and Nymphalidae, including *Caligo*, *Danaus*, *Heliconius* and the electric blue *Morpho* species (see **Plate 1f**), are most popular.

Early on, when butterfly houses emphasized education and conservation, the exhibited butterflies were reared by local people, who sometimes were organized into co-operatives. Production came from tropical countries, including Costa Rica, Kenya and Papua New Guinea. "Ranching" butterflies for export in the pupal stage provides economic benefits and revenue flows to local communities and assists in natural habitat conservation. In East Africa, the National Museums of Kenya, in collaboration with many biodiversity programmes, supported local people of the Arabuko-Sukoke forest-edge in the Kipepeo Project to export harvested butterflies for live overseas exhibit. Self-sustaining since 1999, the project has enhanced income for impoverished people, and supported further nature-based projects including honey production. In Papua New Guinea, village farmers enhance ("ranch") the appropriate vine hosts for butterflies, often on land cleared at the forest edge for their vegetable gardens. Wild adult butterflies emerge from the forest to feed and lay their eggs; hatched larvae feed on the managed vines until harvested at pupation. According to species and conservation legislation, butterflies can be exported live as pupae, or dead as high-quality collector specimens.

Ranching evidently is a "small volume with high unit cost" process, suited best to rare species, and providing dead specimens for collectors in high-value trade. However, the much expanded modern insect zoos and butterfly houses require mass production rearing techniques in order to satisfy the demand for a limited range of species of selected butterflies in high numbers and continuous availablity (see **Plate 1g**). In some tropical countries, such as Costa Rica and Malaysia, commercial facilities have been constructed to provide continuous breeding in confinement from a few founder individuals, providing high-quality pupae in volume for air-freighting to purchasers. Although this is now "large volume with small unit value" production, major farms are likely to be more sustainable ecologically, due to their ability to maintain continuous culture, than are small individual breeders. However, larger suppliers often maintain the link to local butterfly farmers or ranchers. It might be argued that ranching, by potentially depleting wild populations, carries a risk of damage to target species. However, in the Kenyan Kipepeo Project, although preferred lepidopteran species originated from the wild as eggs or early larvae, walk-through visual assessment of butterflies in flight suggested that the relative abundance rankings of species was unaffected despite many years of selective harvest for export. Furthermore, ranching there and in New Guinea builds local support for intact forest as a valuable resource, rather than as "wasted" land to clear for subsistence agriculture.

Of course, irrespective of production method, the translocation of non-native insects for the public to view carries inherent risks. Escape, breeding and establishment outside the native range is a potential problem – not every butterfly is "harmless" and several have larvae that feed on our crops. For example, the attractive Australian orchard swallowtail (*Papilio aegeus*) has larvae that defoliate most species of citrus (lemons, limes, oranges and grapefruit and significant natives), and must be constrained to Australian butterfly houses.

well represented in mythology, including in poem and song. Amber has a long history as jewellery, and the inclusion of insects can enhance the value of the piece.

Most urbanized humans have lost much of this contact with insects, excepting those that share our domicile, such as the cockroaches, tramp ants and hearth crickets that generally arouse antipathy. Nonetheless, exhibits of insects, notably in butterfly farms and insect zoos, are very popular, with millions of people per year visiting such attractions throughout the world (Box 1.2). Insects remain part of Japanese culture, and not only for children; there are insect video games, numerous suppliers of entomological equipment, thousands of personal insect collections, and beetle breeding and rearing is so popular that it can be called beetlemania. In other countries, natural occurrences of certain insects attract ecotourism, including aggregations of overwintering monarch butterflies in coastal central California and in Mexico, the famous glow-worm caves of Waitomo, New Zealand, and Costa Rican locations such as Selva Verde rich in tropical insect biodiversity.

Although insect ecotourism may be limited, other economic benefits are associated with an interest in insects. This is especially so amongst children in Japan, where native rhinoceros beetles (Scarabaeidae, *Allomyrina dichotoma*) sell for a few US$ each, and longer-lived common stag beetles for up to US$10, and may be purchased from automatic vending machines. Adults collect and rear insects with a passion: at the peak of a craze for the large Japanese stag beetle (Lucanidae, *Dorcus curvidens*, called *o-kuwagata*) one could sell for between 40,000 and 150,000 yen (US$300 and US$1250), depending on whether captive reared or taken from the wild. Largest specimens, even if captive reared, fetched several million yen >US $10,000 at the height of the fashion. Such enthusiasm by Japanese collectors can lead to a valuable market for insects from outside Japan. According to official statistics, in 2002 some 680,000 beetles, including over 300,000 each of rhinoceros and stag beetles, were imported, predominantly originating from southern and Southeast Asia. Enthusiasm for valuable specimens extends outside Coleoptera: Japanese and German tourists are reported in the past decade to have purchased rare butterflies in Vietnam for US$1000–2000, which is a huge income for the generally poor local people. Unfortunately, some collectors ignore other countries' legislation (including that of Australia, New Zealand and Himalayan countries) by collecting without permits/licences, taking large numbers of insects and damaging the environment in their desire to harvest them rapidly.

In Asia, particularly in Malaysia, there is interest in rearing, exhibiting and trading in mantises (Mantodea), including orchid mantises (*Hymenopus* species; see sections 13.1.1 and 14.1) and stick-insects (Phasmatodea). Hissing cockroaches from Madagascar and burrowing cockroaches from tropical Australia are reared readily in captivity and can be kept as domestic pets as well as being displayed in insect zoos in which handling the exhibits is encouraged.

Questions remain as to whether wild insect collection, either for personal interest or commercial trade and display, is sustainable. In Japan, although expertise in captive rearing has increased and thus undermined the very high prices paid for certain wild-caught beetles, wild harvesting continues over an ever-increasing region. The possibility of over-collection for trade is discussed in section 1.7, together with other conservation issues.

1.6 CULTURING INSECTS

Many species of insects are maintained routinely in culture for purposes ranging from commercial sale, to scientific research, and even to conservation and reintroduction into the wild. As mentioned in section 1.2, much of our understanding of genetics and developmental biology comes from *Drosophila melanogaster* – a species with a short generation time of about 10 days, high fecundity with hundreds of eggs in a lifetime, and ease of culture in simple yeast-based media. These characteristics allow for large-scale research studies across many generations in an appropriate timescale. Other species of *Drosophila* can be reared in a similar manner, although often requiring more particular dietary requirements, including micronutrients and sterols. *Tribolium* flour beetles (section 1.2) are reared solely on flour. However, many phytophagous insects can be reared only on a particular host plant, in a time- and space-consuming programme, and the search for artificial diets is an important component of applied entomological research. Thus, *Manduca sexta*, the tobacco hornworm, which has provided many physiological insights, including how metamorphosis is controlled, is reared en masse on artificial diets of wheatgerm, casein, agar, salts and vitamins, rather than on any of its diverse natural host plants.

The situation is more complex if host-specific insect parasitoids of pests are to be reared for biological control purposes. In addition to maintaining the pest in quarantine to avoid accidental release, the appropriate life stage must be available for the mass production of parasitoids. The rearing of egg parasitoid *Trichogramma* wasps for biological control of caterpillar pests, which commenced over a century ago, relies on the availability of large numbers of moth eggs. Typically, these come from one of two species, the Angoumois grain moth, *Sitotroga cerealella*, and the Mediterranean flour moth, *Ephestia kuehniella*, which are reared easily and inexpensively on wheat or other grains. The use of artificial media, including insect haemolymph and artificial moth eggs, have been patented as being more efficient egg production methods. However, if host location by parasitoids involves chemical odours produced by damaged tissues (section 4.3.3), such signals are unlikely to be produced by an artificial diet. Thus, mass production of parasitoids against troublesome wood-mining beetle larvae must involve rearing the beetles from egg to adult on appropriately conditioned wood of the correct plant species.

Insects such as crickets, mealworms (tenebrionid beetle larvae) and bloodworms (midge larvae) are mass-reared commercially for feeding to pets, or as bait for anglers. Immature soldier flies can recycle domestic "green" waste and provide feed for chickens and certain pets (see Box 9.1). Furthermore, hobbyists and insect pet owners form an increasing clientele for captive-reared insects such as scarabs and lucanid beetles, mantises, phasmids and tropical cockroaches, many of which can be bred with ease by children following on-line instructions.

Zoos, particularly those with butterfly houses (Box 1.2) or petting facilities, maintain some of the larger and more charismatic insects in captivity. Indeed, some zoos have captive-breeding programmes for certain insects that are endangered in the wild – such as the endangered Lord Howe Island phasmid (*Dryococelus australis*; see **Plate 1c**), a large, flightless stick-insect captive-reared on the island and in Melbourne Zoo (in Australia). In New Zealand, several species of charismatic wetas (outsized, flightless orthopterans; see **Plate 1d**) have been reared in captivity and successfully reintroduced to predator-free offshore islands. Among the greatest successes have been the rearing of several endangered species of butterfly in captivity in Europe and North America, for example by the Oregon Zoo, with eventual releases and reintroductions into restored habitat proving quite successful as interim conservation strategies.

1.7 INSECT CONSERVATION

The major threats to insect biodiversity are similar to those affecting other organisms, namely habitat loss and fragmentation, climate change, and invasive species. Introductions of alien social insects, especially ants (Box 1.3), invasive plants, generalist biological control agents (section 16.5), pathogens, and vertebrate grazers and predators often have led to threats to native insect species. Human-induced changes to climate affect the ranges and phenology of some insect species (section 17.3), but more research is needed on threats to non-pest insects other than butterflies. However, the prime cause of insect declines and extinctions, at least of local populations if not whole species, is the loss of their natural habitats.

Biological conservation typically involves either setting aside large tracts of land for "nature", or addressing and remediating specific processes that threaten large and charismatic vertebrates, such as endangered mammals and birds, or plant species or communities. The concept of conserving habitat for insects, or species thereof, seems of low priority on a threatened planet. Nevertheless, land is reserved and plans exist specifically to conserve certain insects. Such conservation efforts often are associated with human aesthetics, and many (but not all) involve the "charismatic megafauna" of entomology – the butterflies and large, showy beetles. Such charismatic insects can act as "**flagship species**" to enhance wider public awareness and engender financial support for conservation efforts. Flagship species are chosen for their vulnerability, distinctiveness or public appeal, and support for their conservation may help to protect all species that live in the flagship's habitat. Thus, single-species conservation, not necessarily of an insect, is argued to preserve many other species by default, in what is known as the "**umbrella effect**". Somewhat complementary to this is advocacy of a habitat-based approach, which argues for increases in the number and size of protected areas to conserve many insects, which are not (and arguably "do not need to be") understood on a species-by-species basis. No doubt efforts to conserve habitats of native fish globally will preserve, as a spin-off, the much more diverse aquatic insect fauna that depends also upon waters being maintained in

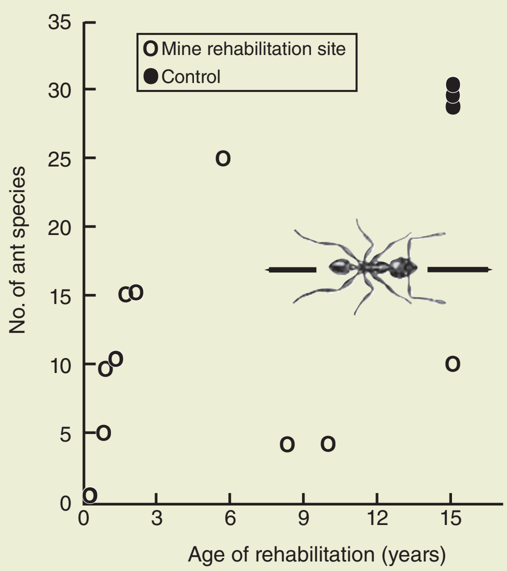
Box 1.3 Tramp ants and biodiversity

No ants are native to Hawai'i, yet there are more than 40 species on the island – all have been brought from elsewhere within the last hundred or so years. In fact, all social insects (honey bees, yellow jackets, paper wasps, termites and ants) on Hawai'i have arrived as the result of human commerce.

Almost 150 species of ants have hitchhiked with us on our global travels and managed to establish themselves outside their native ranges. The invaders of Hawai'i belong to the same suite of ants that have invaded the rest of the world, or seem likely to do so in the near future. From a conservation perspective, one particular behavioural subset of ants is very important, the so-called invasive "tramp" ants. They rank amongst the world's most serious pest species, and local, national and international agencies are concerned with their surveillance and control. The big-headed ant (*Pheidole megacephala*), the long-legged or yellow crazy ant (*Anoplolepis gracilipes*), the Argentine ant (*Linepithema humile*; see **Plate 6e**), the "electric" or little fire ant (*Wasmannia auropunctata*) and tropical fire ants (*Solenopsis* species, especially *S. geminata* and *S. invicta*; see **Plate 6e**) are considered the most serious of these ant pests.

Invasive ant behaviour threatens biodiversity, especially on islands such as Hawai'i, the Galapagos and other Pacific Islands (section 8.7). Interactions with other insects include the protection and tending of aphids and scale insects for their carbohydrate-rich honeydew secretions. This boosts densities of these insects, which include invasive agricultural pests. Interactions with other arthropods are predominantly negative, resulting in aggressive displacement and/or predation on other species, even other tramp ant species encountered. Initial founding is often associated with unstable environments, including those created by human activity. The tendency for tramp ants to be small and short-lived is compensated by year-round increase and rapid production of new queens. Nest-mate queens show no hostility to each other. Colonies reproduce by one or more mated queens plus some workers relocating only a short distance from the original nest – a process known as budding. When combined with the absence of intraspecific antagonism between newly founded and natal nests, colony budding ensures the spreading of a "supercolony" across the ground. Furthermore, some invasive ant species exhibit female parthenogenesis (thelytoky) (section 5.10.1), which is beneficial in founding populations in new areas.

Although initial nest foundation is associated with human or naturally disturbed environments, most invasive tramp species can move into more natural habitats and displace the native biota. Ground-dwelling insects, including many native ants, do not survive the encroachment, and arboreal species may follow into local extinction. Surviving insect communities tend to be skewed towards subterranean species and those with especially thick cuticle such as carabid beetles and cockroaches, which also are chemically defended. Such an impact can be seen from the effects of big-headed ants during the monitoring of rehabilitated sand-mining sites, using ants as indicators (section 9.7). Six years into rehabilitation, as seen in the graph (from Majer 1985), ant diversity neared that found in unimpacted control sites, but the arrival of *Pheidole megacephala* dramatically restructured the system, seriously reducing diversity relative to controls. Even large animals can be threatened by ants – land crabs on Christmas Island, horned lizards in southern California, hatchling turtles in the southeastern United States, and ground-nesting birds everywhere. Invasion by Argentine ants of fynbos, a mega-diverse South African plant assemblage, eliminates ants that specialize in carrying and burying large seeds, but not those that carry smaller seeds (section 11.3.2). Since the vegetation originates by germination after periodic fires, the shortage of buried large seeds is predicted to cause dramatic change to vegetation structure.



Introduced ants are very difficult to eradicate: all attempts to eliminate the red imported fire ant, *Solenopsis invicta*, in the United States have failed, and now a few billion US$ are spent annually on control. This ant also has invaded the West Indies, China and Taiwan, and has spread rapidly. In contrast, it is hoped that an ongoing campaign, costing nearly A$200 million (more than US$150 million) in the first eight years, may prevent *S. invicta* from establishing as an "invasive" species in Australia. The first fire ant sites were found around Brisbane in February 2001, although this ant is suspected to have been present for a number of years prior to its detection. At the height of surveillance, the area infested by fire ants extended to some 80,000 ha. Potential economic damage in excess of A$100 billion over 30 years was estimated if control failed, with inestimable damage to native biodiversity continent-wide. Although intensive searching, baiting, and destruction of nests appear to have been successful in eliminating major infestations, all nests must be eradicated to prevent resurgence, and thus continual monitoring and containment measures are essential. Recent surveying has included the innovative use of an infrared and thermal camera mounted to a helicopter to capture image data during flight that later are analysed by a ground-based computer system "trained" to recognize a fire ant mound's "signature" of reflected energy. Fortunately, incursions of *S. invicta* into New Zealand were detected rapidly and the populations eradicated. Undoubtedly, the best strategy for control of invasive ants is quarantine diligence to prevent their entry, and public awareness to detect accidental entry.

natural condition. Equally, preservation of old-growth forests to protect tree-hole nesting birds such as owls or parrots also will conserve habitat for wood-mining insects that use timber across a complete range of wood species and states of decomposition.

Land that once supported diverse insect communities has been transformed for human agriculture, urban development and to extract resources such as timber and minerals. Many remaining insect habitats have been degraded by the invasion of alien species, both plants and animals, including invasive insects (Box 1.3). The habitat approach to insect conservation aims to maintain healthy insect populations by supporting large patch (habitat) size, good patch quality, and reduced patch isolation. Six basic, interrelated principles serve as guidelines for the conservation management of insects: (i) maintain reserves; (ii) protect land outside of reserves; (iii) maintain quality heterogeneity of the landscape; (iv) reduce contrast between remnant patches of habitat and nearby disturbed patches; (v) simulate natural conditions, including disturbance; and (vi) connect patches of quality habitat. Habitat-based conservationists accept that single-species oriented conservation is important, but argue that it may be of limited value for insects because there are so many species. Furthermore, rarity of insect species may be due to populations being localized in just one or a few places, or in contrast, may be widely dispersed but with low density over a wide area. Clearly, different conservation strategies are required for each case.

Migratory species, such as the monarch butterfly (*Danaus plexippus*), require special conservation. Although the monarch butterfly is not a threatened species, its migration in North America is considered an endangered biological phenomenon by the IUCN (the International Union for the Conservation of Nature). Monarchs from east of the Rockies overwinter in Mexico and then migrate northwards as far as Canada throughout the summer (section 6.7). Critical to the conservation of these monarchs is the safeguarding of the overwintering habitat at Sierra Chincua and elsewhere in Mexico. A highly significant insect conservation measure implemented in recent years is the decision of the Mexican government to support the Monarch Butterfly Biosphere Reserve (Mariposa Monarca Biosphere Reserve), which was established to protect this phenomenon. Another major threat to monarch butterflies is loss of larval breeding sites in North America (discussed in section 16.6.1). Efforts to monitor monarch populations in North America involve citizen scientists (Box 1.1). Successful conservation of this flagship butterfly requires collaborations involving the United States, Canada and Mexico, to ensure protection of both overwintering sites and migration flyway habitats. However, preservation of western overwintering populations in coastal California conserves no other native species. The reason for this is that the major resting sites are in groves of large, introduced eucalypt trees, especially blue gums, which have a depauperate fauna in their non-native habitat.

A successful example of single-species conservation involves the endangered El Segundo blue butterfly, *Euphilotes battoides* ssp. *allyni*, whose principal colony in sand dunes near Los Angeles airport was threatened by urban sprawl and golf-course development. Protracted negotiations with many interested parties resulted in designation of 80 hectares as a reserve, sympathetic management of the golf course "rough" for the larval food plant *Erigonum parvifolium* (buckwheat), and control of alien plants plus limitation on human disturbance. Southern Californian coastal dune systems are seriously endangered habitats, and management of this reserve for the El Segundo blue conserves other threatened species.

Land conservation for butterflies is not an indulgence of affluent southern Californians: the world's largest butterfly, the Queen Alexandra's birdwing, *Ornithoptera alexandrae*, of Papua New Guinea, provides a success story from the developing world. This spectacular species, whose caterpillars feed only on *Aristolochia dielsiana* vines, is endangered and limited to a small area of lowland rainforest in northern Papua New Guinea. Under Papua New Guinean law, this birdwing species has been protected since 1966, and international commercial trade was banned by listing it on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). The Queen Alexandra's birdwing has acted as a flagship species for conservation in Papua New Guinea, and its initial conservation success attracted external funding for surveys and reserve establishment. Conserving Papua New Guinean forests for this and related birdwings undoubtedly results in conservation of much diversity under the umbrella effect, but mining and corrupt large-scale logging in Papua New Guinea in the past two decades threatens much of rainforests there.

As discussed in Box 1.2, Kenyan and New Guinean insect conservation efforts have some commercial incentives and provide impoverished people with some recompense for their protection of natural environments. However, commerce need not be the sole motivation: the aesthetic appeal of having native birdwing butterflies flying wild in local neighbourhoods, combined with local education programmes in schools and communities, are helping to save the subtropical Australian Richmond birdwing butterfly, *Ornithoptera richmondia* (see **Plate 1e**). Larval Richmond birdwings develop on two species of native *Pararistolochia* vines and require large plants to satisfy their appetite. However, about two-thirds of the original coastal rainforest habitat supporting native vines has been lost, and the alien South American *Aristolochia elegans* ("Dutchman's pipe"), introduced as an ornamental plant and escaped from gardens, lures females to lay eggs on it as a prospective host. This oviposition mistake is deadly since toxins of this plant kill young caterpillars. This conservation problem has been addressed by an education programme to encourage the removal of Dutchman's pipe vines from native vegetation, from sale in nurseries, and from gardens and yards. Replacement in bush and gardens with native *Pararistolochia* was encouraged after a massive effort to propagate the vines. Birdwing populations isolated by habitat fragmentation also suffer inbreeding depression, which is being alleviated by planting corridors of suitable host plants and by captive breeding and reintroduction of genetically diverse individuals. Although recovery of the birdwing population was impacted by continued loss of habitat and years of drought, wetter conditions from 2010 improved foodplant quality and, combined with a renewed cultivation effort, led to the first population increases following a century of decline. However, habitat loss continues and ongoing community action throughout the native range of the Richmond birdwing is necessary to reverse its decline.

The idea that concerned citizens can conserve insects by management of their gardens (backyards) has gained acceptance, notably with regard to bee decline. Guidance is available, including from "show gardens", for developing a pollinator-friendly garden by growing selected plants, emphasizing nectar-producers such as borage (which is best for honey bees), lavender (for bumblebees) and marjoram (an all-round attractant to all bees and hoverflies). With increasing enthusiasm for local/urban honey-bee hives, sustainability can be attained only by increasing flowering plants in gardens and public spaces to provide food sources for a diversity of insects.

Butterflies and bees, being familiar insects with nonthreatening lifestyles, are flagships for invertebrate conservation. However, certain orthopterans, including New Zealand wetas, have been afforded legal protection, and conservation plans exist for dragonflies and other freshwater insects in the context of conservation and management of aquatic environments, and there are plans for firefly (beetle) and glow worm (fungus gnat) habitats. Agencies in certain countries have recognized the importance of retention of fallen dead wood as insect habitat, particularly for long-lived wood-feeding beetles.

Designation of reserves for conservation, seen by some as the answer to threat, rarely is successful without understanding species requirements and responses to management. The butterfly family Lycaenidae (blues, coppers and hairstreaks), with some 6000 species, comprises over 30% of the butterfly diversity. Many have relationships with ants (e.g. as inquilines; section 12.3), some being obliged to pass some or all of their immature development inside ant nests, others are tended on their preferred host plant by ants, yet others are predators on ants and scale insects, while being tended by ants. These relationships can be very complex, and may be rather easily disrupted by environmental changes, leading to threats to the butterflies. Certainly in Western Europe, species of Lycaenidae figure prominently on lists of threatened insect taxa. Notoriously, the decline of the large blue butterfly *Phengaris* (formerly *Maculinea*) *arion* in England was blamed upon over-collection, but see Box 1.4 for a different interpretation. Action plans

Box 1.4 Conservation of the large blue butterfly

The large blue butterfly, *Phengaris* (formerly *Maculinea*) *arion* (Lepidoptera: Lycaenidae), was reported to be in serious decline in southern England in the late 19th century, a phenomenon ascribed then to poor weather. By the mid-20th century, this attractive species was restricted to some 30 colonies in southwest England. Few colonies remained by 1974 and the estimated adult population had declined from about 100,000 in 1950 to 250 in some 20 years. Final extinction of the species in England in 1979 followed two successive hot, dry breeding seasons. Since the butterfly is beautiful and highly sought by collectors, excessive collecting was presumed to have caused at least the long-term decline that made the species vulnerable to deteriorating climate. This decline occurred even though a reserve was established in the 1930s to exclude both collectors and domestic livestock, in an attempt to protect the butterfly and its habitat.

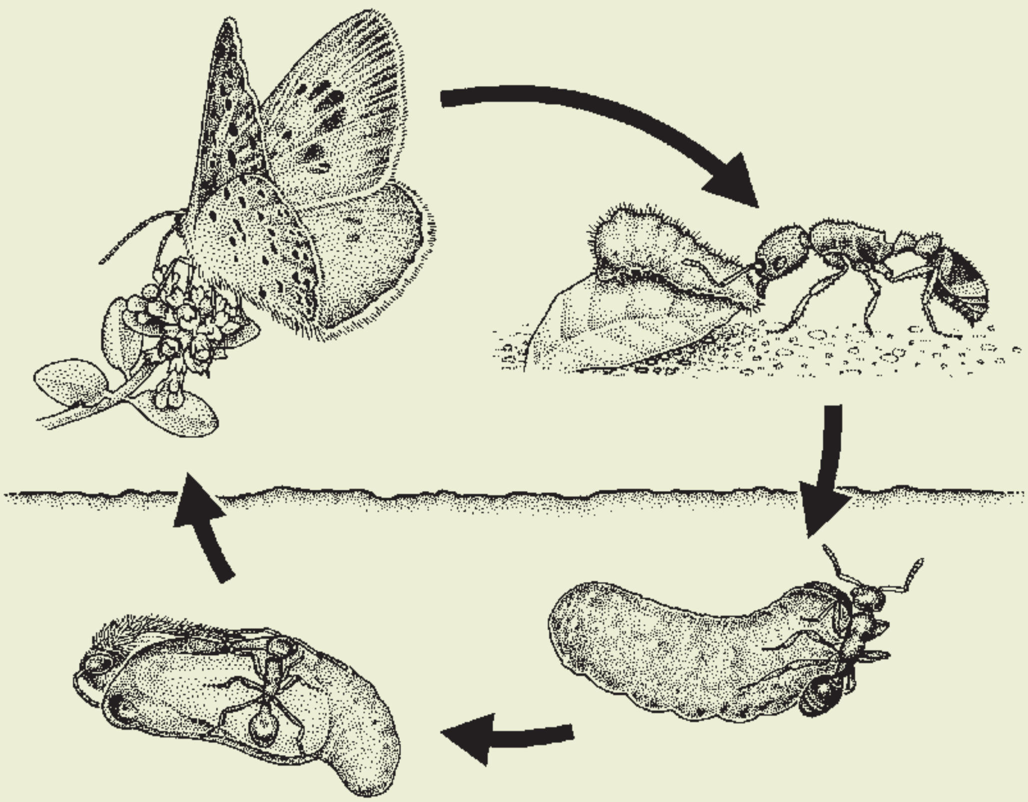
Evidently, habitat had changed through time, including a reduction of wild thyme (*Thymus praecox*), which provides the food for early instars of the large blue's caterpillar. Shrubbier vegetation replaced short-turf grassland because of loss of grazing rabbits (through disease) and the exclusion of grazing cattle and sheep from the reserved habitat. Thyme survived, however, but the butterflies continued to decline to extinction in Britain.

A more complex story has since been revealed by research associated with the reintroduction of the large blue to England from continental Europe. The larva of the large blue butterfly in England and on the European continent is an obligate predator in colonies of red ants belonging to species of *Myrmica*. Larval large blues must enter a *Myrmica* nest, in which they feed on larval ants. Similar predatory behaviour, and/or tricking ants into feeding them as if they were the ants' own brood, are features in the natural history of many Lycaenidae (blues and coppers) worldwide (section 1.7 and section 12.3). After hatching from an egg laid on the larval food plant, the large blue's caterpillar feeds on thyme flowers until the moult into the final (fourth) larval instar, around August. At dusk, the caterpillar drops to the ground from the natal plant, where it waits inert until a *Myrmica* ant finds it. The worker ant attends the larva for an extended period, perhaps more than an hour, during which it feeds from a sugar gift secreted from the caterpillar's dorsal nectary organ. At some stage, the caterpillar becomes turgid and adopts a posture that seems to convince the tending ant that it is dealing with an escaped ant brood, and it is carried into the nest. Until this stage, immature growth has been modest, but in the ant nest the caterpillar becomes predatory on ant eggs and larvae and grows rapidly. The caterpillar spends winter in the ant nest and, 9–10 months after it entered the nest, pupates in early summer of the following year. The caterpillar requires an average 230 immature ants for successful pupation. It apparently escapes predation by the ants by secreting surface chemicals that mimic those of the ant brood, and probably receives special treatment in the colony by producing sounds that mimic those of the queen ant (section 12.3). The adult butterfly emerges from the pupal cuticle in summer, and departs rapidly from the nest before the ants identify it as an intruder.

Adoption and incorporation into the ant colony turns out to be the critical stage in the life history. The complex system involves the "correct" ant, *Myrmica sabuleti*, being present, and this in turn depends on the appropriate microclimate associated with short-turf grassland. Longer grass causes cooler near-soil microclimate conditions, favouring other *Myrmica* species, including *M. scabrinodes*, which may displace *M. sabuleti*. Although caterpillars associate apparently indiscriminately with any *Myrmica* species, survivorship differs dramatically: with *M. sabuleti* approximately 15% survive, but an unsustainable reduction to <2% survivorship occurs with *M. scabrinodes*. Successful maintenance of large blue populations requires that >50% of the adoption by ants must be by *M. sabuleti*.

Other factors affecting survivorship include the requirements for the ant colony to have no alate (winged) queens and have at least 400 well-fed workers to provide enough larvae for the caterpillar's feeding needs, and to lie within 2 m of the host thyme plant. Such nests are associated with newly burnt grasslands, which are rapidly colonized by *M. sabuleti*. Nests should not be so old as to have developed more than the founding queen: the problem here being that with numerous alate queens in the nest, the caterpillar can be mistaken for a queen and attacked and eaten by nurse ants.

Now that we understand the intricacies of the relationship, we can see that the well-meaning creation of reserves that lacked rabbits and excluded other grazers created vegetation and microhabitat changes that altered the dominance of ant species, to the detriment of the butterfly's complex relationships. Over-collecting is not implicated, although on a broader scale climate change must be significant. Now, five populations originating from Sweden have been reintroduced to habitat and conditions appropriate for *M. sabuleti*, thus leading to thriving populations of the large blue butterfly. Interestingly, other rare species of insects in the same habitat have responded positively to this informed management, suggesting perhaps an umbrella role for the butterfly species.



in Europe for the reintroduction of this and related species, and appropriate conservation management of *Phengaris* species, have been put in place: these depend vitally upon a species-based approach. Only with understanding of general and specific ecological requirements of conservation targets can appropriate management of habitat be implemented.

The impediments to insect conservation are multifaceted and include poor public perception of the ecological importance of invertebrates, limited knowledge of their species diversity, distributions and abundance in space and time, and paucity of information on their sensitivity to changes in habitat. As discussed earlier, policymakers and land managers often assume that the protection of habitat for vertebrates will conserve resources for invertebrates under an umbrella effect. Clearly, we need more information on the effectiveness for insects and other invertebrates of conservation measures designed primarily for vertebrates and plants. Funding for comprehensive entomological surveys or experimental studies is always limited, but the identification and detailed study of suitable indicator or surrogate taxa can provide helpful guidelines for conservation decisions involving insects. Furthermore, valuable data on insect abundance, distributions and phenology can derive from citizen science programmes (Box 1.1).

1.8 INSECTS AS FOOD

1.8.1 Insects as human food: entomophagy

In this section we review the increasingly popular topic of insects as human food. Nearly 2000 species of insects in more than 100 families are, or have been, used for food somewhere in the world, especially in central and southern Africa, Asia, Australia and Latin America. Food insects generally feed on either living or dead plant matter, and chemically protected species are avoided. Termites, crickets, grasshoppers, locusts, beetles, ants, bee brood and moth larvae are frequently consumed insects. It is estimated that insects form part of the traditional diets of at least two billion people, but the ever-increasing human population and demand for food is causing over-exploitation of some wild edible insects. Although insects are high in protein, energy and various vitamins and minerals, and can form 5–10% of the annual animal protein consumed by certain indigenous peoples, western society essentially overlooks entomological cuisine.

Typical “western” repugnance of entomophagy is cultural rather than scientific or rational. After all, other invertebrates such as certain crustaceans and molluscs are considered to be desirable culinary items. Objections to eating insects cannot be justified on the grounds of taste or food value. Many have a nutty flavour and studies report favourably on the nutritional content of insects, although their amino acid and fatty acid compositions vary considerably among different food-insect species.

Mature larvae of palm weevils, *Rhynchophorus* species (Coleoptera: Curculionidae), have been appreciated by people in tropical Africa, Asia and the Neotropics for centuries. These fat, legless “palmworms” (see **Plate 2a**) provide a rich source of animal fat, plus substantial amounts of riboflavin, thiamine, zinc and iron. Primitive cultivation systems involve wounding or felling palm trees to provide suitable food for the weevils. Such cultivation occurs in South America (Brazil, Colombia, Paraguay and Venezuela) and parts of Southeast Asia. Commercial facilities have been constructed in Thailand to raise the grubs on macerated (“chipped”) palm trunk and leaf-base tissues. However, throughout Asia, palmworms are pests that damage and kill coconut and oil palm trees in plantations. From this part of the world a *Rhynchophorus* species entered California, USA, threatening ornamental and date palms (Box 1.5).

In Africa, people eat many species of moth caterpillars that provide a rich source of iron and have high calorific value, with a protein content ranging from 45 to 80%. In Zambia, the edible caterpillars of emperor moths (Saturniidae), locally called *mumpa*, provide a valuable dietary supplement of fresh, fried, boiled or sun-dried larvae that offsets malnutrition caused by protein deficiency. Caterpillars of *Gonimbrasia belina* (Saturniidae) (see **Plate 2b**), called mopane, mopanie, mophane or phane, are utilized widely. They develop on the widespread mopane, a leguminous tree (*Colophospermum mopane*) that grows in a wide belt of open forest (“mopane woodland” landscape) across southern Africa (Fig. 1.2). Caterpillars are hand picked by poor rural women for family subsistence. The de-gutted insects are boiled or sometimes salted and dried, after which they contain about 50% protein and 15% fat – approximately twice the values for cooked beef. However, organized teams, largely of men,

Box 1.5 Palmageddon? Weevils in the palms

Residents of upmarket Laguna Beach in Orange County, southern California, are losing the ornamental palm trees that provide landscape features in this and other Mediterranean-climate communities (as illustrated here). In August 2010, a large dying Canary Island date palm (*Phoenix canariensis*) was felled by arborists and found to be infested with weevils. The culprit was believed initially to be *Rhynchophorus ferrugineus*, the red palm weevil (see **Plate 2a**), that was causing problems already in Asia, the Middle East and Mediterranean Europe, but this was the first report of the pest in North America. Given that California's date industry is valued at US$30 million, and ornamental palm tree sales at $70 million per year in California and $127 million in Florida, a research programme was commenced without delay.

The programme exemplifies many issues in insect biology associated with control of introduced pests. First, it was necessary to establish the size of the affected area. It is very unlikely that the first insects to be noticed are those that invaded: the public is rarely vigilant to early infestations, especially when symptoms may occur several years after arrival, and skilled specialists are ever-more thinly spread. Usually, arrival times of first invaders are estimated to have been several (too many) years prior to official recognition. Recruits had to be mobilized and trained to recognize the damage symptoms, and some form of automated trapping had to be developed and distributed in Laguna Beach and surrounds.

Since these weevils already were killing palms elsewhere in the world, researchers travelled to see how others coped with the problem, and also to observe the weevils in their native areas. The bad news was that the invasions in the Middle East and Mediterranean Europe were serious, spreading and uncontrolled. For example, since 2004 the south of France had been dealing with the weevils, which had spread along the Riviera to the Pyrenees and even to Corsica. Even the iconic palms that provide the backdrop to images of the Cannes Film Festival are dying. The good news was that an airborne lure that combined essence of damaged palms and weevil communication chemicals

(pheromones; section 4.3.2) had been developed already. This cocktail could be used to monitor the flying adult weevils in California, and potentially trap enough to exert some level of population control (section 16.9). California had some advantages, notably that the problems seemed restricted to Laguna Beach, and despite a crippling recession, a research budget was found quickly and implemented. Although total destruction by chipping the complete palm was the only method of control, residents were "on-side" with the programme.

In an unexpected twist, it turned out that the weevil that had entered the Golden State was not the globally invasive red palm weevil *R. ferrugineus*, but the differently pigmented (a black form with a red stripe) but otherwise similar, *R. vulneratus*. This revised identification, supported by molecular evidence for its distinction from red palm weevil, allows better identification of the natural source area, where its biology, including control can be studied (for more on biological control, see section 16.5), and explains some subtle differences in behaviour relative to the red palm weevil. The red stripe form of the weevil is native to Bali, Indonesia, where the larvae are considered to be such a "live" food delicacy that coconuts, sago and nipa (nypa) palms are damaged deliberately to induce weevil infestation, from which the tasty larvae are harvested. However, the occurrence of *R. vulneratus* in California does raise the question of how the weevils got there – this might have been explained more easily had the invader been the widespread and clearly invasive red palm weevil. It seems highly unlikely that a species otherwise restricted to Indonesia should arrive unaided on the opposite side of the Pacific Ocean and only in a solitary suburban location. Undoubtedly, a breach of biosecurity had occurred, yet it seems improbable that the "usual route" was responsible; that is, the legal (or otherwise) importation of infested host plants (large coconut or sago palms in this case). Scientists studying the situation suspect the demand for the weevil larvae as food led to illegal import of live weevils as a gastronomic souvenir. Perhaps the Californian dietary interest in locavory (eating local produce) could extend to include palm grubs? More seriously, can Californians imagine life without native palms dotting the landscape, and no palms in Palm Springs and no dates from the Coachella Valley?

now harvest intensively for commercial sale (mopane are available in certain urban supermarkets) and this increased demand has degraded a common property resource to an over-exploited and unsustainable "free-for-all" resource. Demand, especially from urban South Africa, has led to forest damage and localized moth extinction, including in Botswana. An optimistic sign of sustainability is a trial in Kruger National Park, where local people from Limpopo Province are supervised while they collect mopane worms within the park during a short, pre-Christmas season.

In the Philippines, June beetles (melolonthine scarabs), weaver ants (*Oecophylla smaragdina*) (see **Plate 6b**), mole crickets, palmworms (weevil larvae; Box 1.5, see also **Plate 2a**) and locusts are eaten in some regions. Locusts form an important dietary supplement during outbreaks, which apparently have become less common since the widespread use of insecticides. Various species of grasshoppers and locusts were eaten commonly by native tribes in western North America prior to the arrival of Europeans. The number and identity of species used have been poorly documented, but species of *Melanoplus* were among those consumed. Harvesting involved driving grasshoppers into a pit in the ground using fire or advancing people, or herding them into a bed of coals. Today, people in Central America, especially Mexico, harvest, sell, cook and consume grasshoppers.

Australian Aborigines use (or once used) a wide range of insect foods, especially moth larvae. The caterpillars of wood or ghost moths (Cossidae and Hepialidae) (Fig. 1.3, see also **Plate 2c**) are called witchety grubs, from the Aboriginal word "witjuti" for the *Acacia* species (wattles), on the roots and stems of which the grubs feed. Witchety grubs, which are regarded as a delicacy, contain 7–9% protein, 14–38% fat and 7–16% sugars, as well as being good sources of iron and calcium. Adults of the bogong moth, *Agrotis infusa* (Noctuidae), formed another important Aboriginal food, once collected in their millions from aestivating sites in narrow caves and crevices on mountain summits in southeastern Australia. Moths cooked in hot ashes provided a rich source of dietary fat.

Aboriginal people living in central and northern Australia eat the contents of the apple-sized galls of *Cystococcus pomiformis* (Hemiptera: Eriococcidae), commonly called bush coconuts or bloodwood apples (see **Plate 4f,g**). These galls occur only on bloodwood eucalypts (*Corymbia* species) and can be very abundant after a favourable growing season. Each mature gall

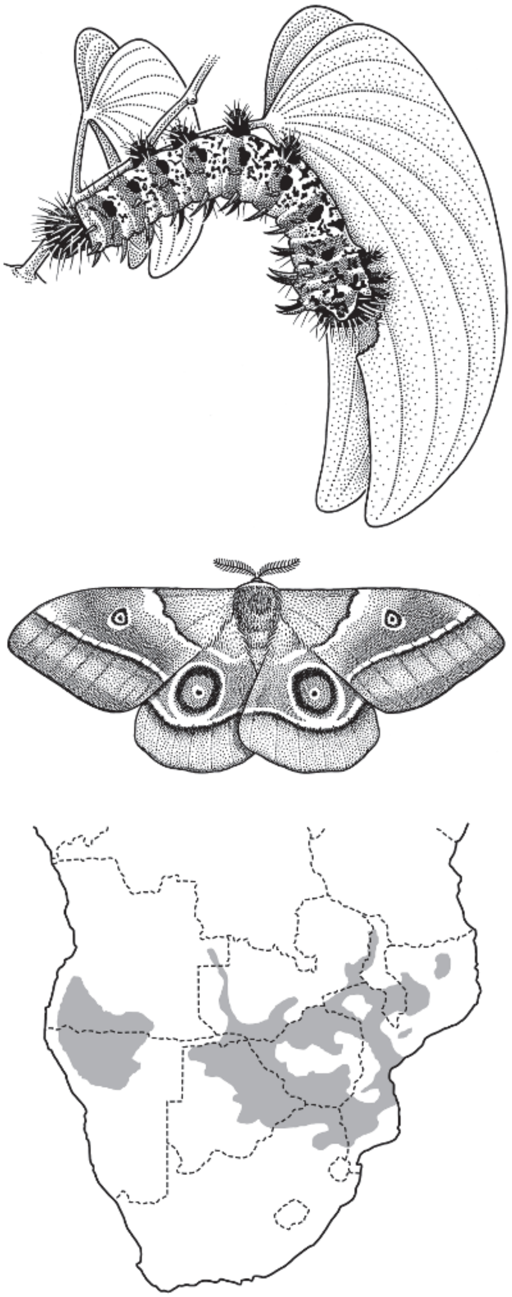


Fig. 1.2 Mopane moths and host tree. (a) Larva of *G. belina* on mopane (*Colophospermum mopane*) leaves. (b) Adult of *Gonimbrasia belina*. (c) Distribution of mopane woodland in southern Africa. (After photographs by R.G. Oberprieler and map from van Voortthuizen 1976.)

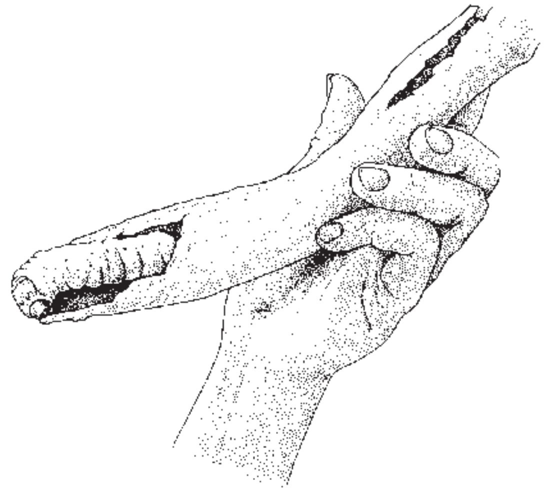


Fig. 1.3 A delicacy of the Australian Aborigines – a witchety (or witjuti) grub, a caterpillar of a wood moth (Lepidoptera: Cossidae) that feeds on the roots and stems of witjuti bushes (certain *Acacia* species). (After Cherikoff & Isaacs 1989.)

contains a single adult female, up to 4 cm long, which is attached by her mouth area to the base of the inner gall and has part of her abdomen plugging a hole in the gall apex. The inner wall of the gall is lined with white edible flesh, about 1 cm thick, which serves as the feeding site for the male offspring of the female. Aborigines relish the watery female insect and her nutty-flavoured nymphs, then scrape out and consume the white coconut-like flesh of the inner gall.

A favourite source of sugar for Australian Aboriginals living in arid regions comes from species of *Melophorus* and *Camponotus* (Formicidae), popularly known as honeypot ants (**Plate 2g–h**). Specialized workers (called repletes) store nectar, fed to them by other workers, in their huge distended crops (see Fig. 2.4). Repletes serve as food reservoirs for the ant colony and regurgitate part of their crop contents when solicited by another ant. Aborigines dig repletes out from their underground nests, an activity most frequently undertaken by women, who may excavate pits to a depth of a metre or more in search of these sweet rewards. Individual nests rarely supply more than 100 g of a honey that is essentially similar in composition to commercial honey. Honeypot ants in the western United States and Mexico belong to a different genus, *Myrmecocystus*. The repletes, a highly valued food, are collected by the rural people of Mexico, a difficult process in the hard soil of the stony ridges where the ants nest.

Perhaps the general western rejection of entomophagy is only an issue of marketing being required to counter a popular perception that insect food is for the poor and protein-deprived of the developing world. In reality, certain sub-Saharan Africans apparently prefer caterpillars to beef. Ant grubs (so called "ant eggs") and eggs of water boatmen (Corixidae) and backswimmers (Notonectidae) are much sought after in Mexican gastronomy as "caviar". In parts of Asia, a diverse range of insects can be purchased (see **Plate 2d–f**). Traditionally, desirable water beetles for human consumption are valuable enough to be farmed in Guangdong. The culinary culmination may be the meat of the giant water bug *Lethocerus indicus* or the Thai and Laotian *mangda* sauces made with the flavours extracted from the male abdominal glands, for which high prices are paid. Even in the urban United States some insects may become popular as a food novelty. The millions of 17-year cicadas that periodically plague northeastern states are edible. Newly hatched cicadas, called tenerals, are best for eating because their soft body cuticle means that they can be consumed without first removing the legs and wings. These tasty morsels can be marinated or dipped in batter and then deep-fried, boiled and spiced, roasted and ground, or stir-fried with favourite seasonings.

Large-scale harvest or mass production of insects for human consumption brings some practical and other problems. The small size of most insects presents difficulties in collection or rearing and in processing for sale. The unpredictability of many wild populations needs to be overcome by the development of culture techniques, especially as over-harvesting from the wild could threaten the viability of some insect populations. Another problem is that not all insect species are safe to eat. Warningly coloured insects are often distasteful or toxic (Chapter 14) and some people can develop allergies to insect material (section 15.6.3). However, several advantages derive from eating insects. The encouragement of entomophagy in many rural societies, particularly those with a history of insect use, may help diversify peoples' diets. By incorporating mass-harvesting of pest insects into control programmes, the use of pesticides can be reduced. Furthermore, if carefully regulated, cultivating insects for protein should be less environmentally damaging than cattle ranching, which devastates forests and native grasslands. Insect farming (the rearing of mini-livestock) is compatible with low-input sustainable agriculture and most insects have a high food conversion efficiency compared with conventional meat animals. However, the unregulated harvesting of wild insects can, and is, causing conservation concerns, especially in parts of Asia and Africa, where populations of some edible insects are threatened by over-collection as well as by habitat loss.

1.8.2 Insects as feed for domesticated animals

Although many people do not relish the prospect of eating insects, the concept of insects as a protein source for domesticated animals is quite acceptable. The nutritive significance of insects as feed for fish, poultry, pigs, and farm-grown mink certainly is recognized in China, where feeding trials have shown that insect-derived diets can be cost-effective alternatives to more conventional fishmeal diets. The insects involved are primarily the pupae of silkworms (*Bombyx mori*), the larvae and pupae of house flies (*Musca domestica*), and the larvae of mealworms (*Tenebrio molitor*). The same or related insects are being used or investigated elsewhere, particularly as poultry or fish feedstock. Silkworm pupae, a by-product of the silk industry, provide a high-protein supplement for chickens. In India, poultry are fed the meal that remains after the oil has been extracted from the pupae. Fly larvae fed to chickens can recycle animal manure, and development of insect recycling systems for converting organic wastes into feed supplements is ongoing (see Box. 9.1).

Clearly, insects have the potential to form part of the nutritional base of people and their domesticated animals. Further research is needed, and a database with accurate identifications is required to handle biological information. We must know which species we are dealing with in order to make use of information gathered elsewhere on the same or related insects. Data on the nutritional value, seasonal occurrence, host plants, or other dietary requirements, and rearing or collecting methods must be collated for all actual or potential food insects. Opportunities for insect food enterprises are numerous, given the immense diversity of insects.

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