Third Edition

THE INSECTS

AN OUTLINE OF ENTOMOLOGY

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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 concerning 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, provided by bees (or specialized ants). Insects pollinate our crops. Many insects share our houses, agriculture, and food stores. Others live on us, our domestic pets, or our livestock, and yet 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 of 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 below, 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 past and some continuing cultural and economic aspects of insects, their aesthetic and tourism appeal, and their importance as foods for humans and animals. We conclude with a review of the conservation significance of insects.

1.1 WHAT IS ENTOMOLOGY?

Entomology is the study of insects. Entomologists, the people who study insects, observe, collect, rear, and experiment with insects. Research undertaken by entomologists covers the total range of biological disciplines, including evolution, ecology, behavior, 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 availability of ground-glass optics made the study of insects acceptable for the thoughtful privately wealthy. Although people working with insects hold professional positions, many aspects of the study of insects remain suitable for the hobbyist. Charles Darwin's initial enthusiasm in natural history was as a collector of beetles (as shown in the vignette for this chapter). All his life he continued to study insect evolution and communicate with amateur entomologists throughout the world. Much of our present understanding of worldwide insect diversity derives 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 Henri Fabre in observing close-up activities of insects. We can discover much of scientific interest at little expense concerning the natural history of even "well known" insects. The variety of size, structure, and color in insects (see Plates 1.1–1.3, facing p. 14) is striking, whether depicted in drawing, photography, or film.

A popular misperception is that professional entomologists emphasize killing or at least controlling insects, but in fact entomology includes many positive aspects of insects because their benefits to the environment outweigh their harm.

1.2 THE IMPORTANCE OF INSECTS

We should study insects for many reasons. Their ecologies are incredibly variable. Insects may dominate food chains and food webs in both volume and numbers. Feeding specializations of different insect groups include ingestion of detritus, rotting materials, living and dead 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 condi-

tions, 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 parasitism 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 "keystones" because loss of their critical ecological functions could collapse 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 provide us with honey but are also valuable agricultural pollinators worth an estimated several billion US$ annually in the USA. Estimates of the value of non-honey-bee pollination in the USA could be as much as $5–6 billion per year. The total value of pollination services rendered by all insects globally has been estimated to be in excess of $100 billion annually (2003 valuation). 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.

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. Silk from the cocoons of silkworm moths, *Bombyx mori*, and related species has 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 of finding novel chemicals.

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 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 behaviors 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 (grains) and number of individuals of flour beetles (*Tribolium* spp.) in culture, combined with their short life history (compared to mammals, for example), gave insights into mechanisms regulating populations. Some early holistic concepts in ecology, for example ecosystem and niche, came from scientists studying freshwater systems where insects dominate. Alfred Wallace (depicted in the vignette of Chapter 17), the independent and contemporaneous discoverer with Charles Darwin of the theory of evolution by natural selection, based his ideas on observations of tropical insects. Theories concerning the many forms of mimicry and sexual selection have been derived from observations of insect behavior, which continue to be investigated by entomologists.

Lastly, 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 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 nearly 250,000 described species, with the Diptera and Lepidoptera having between 125,000 and 150,000 species, and Hemiptera approaching 95,000. Of the remaining orders of living insects, none exceed the 20,000 described species of the Orthoptera (grasshoppers, locusts, crickets, and katydids). Most of the "minor" orders have from 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 less than 2000 described species and the ubiquitous cockroaches belong to an order (Blattodea) with only 4000 species. Nonetheless, 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 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, allocation to feeding 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 Papua New Guinean tropical forest, seems very much less than estimated early 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 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 exist, realistically could only be amongst the Coleoptera, drab-colored Lepidoptera, phytophagous Diptera, and parasitic Hymenoptera.

Some (but not all) recent re-analyses tend towards lower estimates derived from taxonomists' calculations and extrapolations from regional sampling rather than those derived from ecological scaling: a figure of between four 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 insects 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 the inverse relationship between the distribution of entomologists interested in biodiversity issues (the temperate northern hemisphere) and the centers of richness of the insects themselves (the tropics and southern hemisphere).

Studies in tropical American rainforests suggest much undescribed novelty in insects comes from the beetles, which provided the basis for the original high richness estimate. Although beetle dominance may be true in places such as the Neotropics, this might be an artifact of the collection and research biases of entomologists. In some well-studied temperate regions such as Britain and Canada, species of true flies (Diptera) appear to outnumber beetles. Studies of canopy insects of 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 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 provides one meal to a giraffe, may support 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 can be said to be more fine-grained from an insect 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
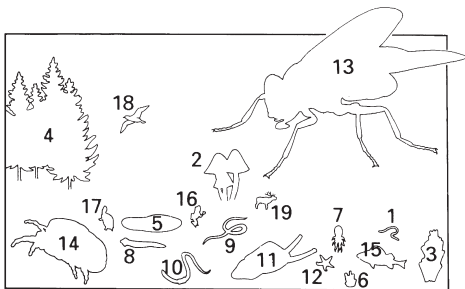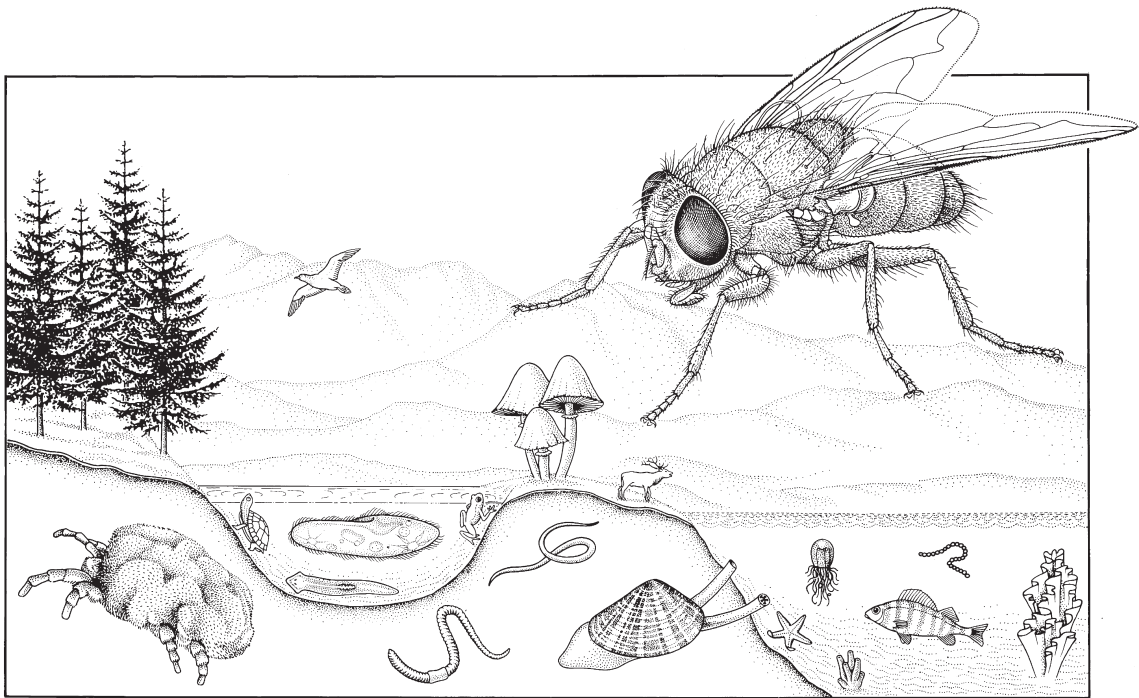
1 Prokaryotes
2 Fungi
3 Algae
4 Plantae (multicellular plants)

5 Protozoa
6 Porifera (sponges)
7 Cnidaria (jellyfish, corals, etc.)
8 Platyhelminthes (flatworms)
9 Nematoda (roundworms)
10 Annelida (earthworms, leeches, etc.)
11 Mollusca (snails, bivalves, octopus, etc.)
12 Echinodermata (starfish, sea urchins, etc.)
13 Insecta
14 Non-insect Arthropoda
15 Pisces (fish)
16 Amphibia (frogs, salamanders, etc.)
17 Reptilia (snakes, lizards, turtles)
18 Aves (birds)
19 Mammalia (mammals)

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.)

sensory and neuro-motor systems more comparable to those of vertebrate animals than 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 potential 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. 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 (section 5.3) may lead to rapid alteration in intra-specific communication. When (or if) the isolated population rejoins the larger parental population, altered sexual signaling deters hybridization and the identity of each population (incipient species) is maintained in 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 behavior.

Comparisons amongst and between insects and their close relatives suggest reasons for insect diversity. We can ask what are the shared characteristics of 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 of these factors are explored in Chapter 8). In contrast to the most speciose insect groups, arach-

nids lack winged flight, complete transformation of body form during development (metamorphosis) and dependence on specific food organisms, and are not phytophagous. Exceptionally, mites, the most diverse and abundant of arachnids, have many very specific associations with other living organisms.

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 around 0.3 mm of mymarid wasps (parasitic on eggs of insects) being unexceptional. At the other extreme, the greatest wingspan of 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 insects were appreciably larger than their extant relatives. For example, an Upper Carboniferous silverfish, *Ramsdelepidion schusteri* (Zygentoma), had a body length of 6 cm 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* (Protodonata), had a wingspan of 71 cm. Notably amongst these large insects, the great size comes predominantly with a narrow, elongate body, although one of the heaviest extant insects, the 16 cm long hercules beetle *Dynastes hercules* (Scarabaeidae), is an exception in having a bulky body.

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 (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 section 8.2.1.

In summary, many insect radiations probably depended upon (a) the small size of individuals, combined with (b) short generation time, (c) sensory and neuro-motor sophistication, (d) evolutionary interactions with plants and other organisms, (e) metamorphosis, and (f) 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 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 fulfill this need: the same insects even may have different vernacular names amongst peoples that speak the same language. For instance, the British refer to "ladybirds", whereas the same coccinellid beetles are "ladybugs" to many people in the USA. Many insects have no vernacular name, or one common name is given to many species as if only one is involved. These difficulties are addressed by the Linnaean system, which provides every described species with two given names (a binomen). The first is the generic (genus) name, used for a usually broader grouping than the second name, which is the specific (species) name. These latinized names are always used together and are italicized, as in this book. The combination of generic and specific 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 17.3.2).

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 textbook, 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 generic 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,

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

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

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 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 some group names can be recognized by inspection of the ending (Table 1.1).

Depending on the classification system used, some 30 orders of Insecta are 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 (Chapter 7). Orders have been recognized rather arbitrarily in the past two centuries, and the most that can be said is that presently constituted orders contain

similar insects differentiated from other insect groups. Over time, a relatively stable classification system has developed but differences of opinion remain as to the boundaries around groups, with "splitters" recognizing a greater number of groups and "lumpers" favoring 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 (Fig. 7.2). The order Hemiptera sometimes was divided into two orders, Homoptera and Heteroptera, but the homopteran grouping is invalid (non-monophyletic) and we advocate a different classification for these bugs shown stylized on our cover and in detail in Fig. 7.5 and Box 11.8.

In this book we recognize 30 orders for which the physical characteristics and biologies of their constituent taxa are described, and their relationships considered (Chapter 7). Amongst these orders, we distinguish "major" orders, based upon the numbers of species being much higher in Coleoptera, Diptera, Lepidoptera, Hymenoptera, and Hemiptera than in the remaining "minor" orders. Minor orders often have quite homogeneous ecologies which can be summarized conveniently in single descriptive/ecological boxes following the appropriate ecologically based chapter (Chapters 9–15). The major orders are summarized ecologically less readily and information may appear in two chapters. A summary of the diagnostic features of all 30 orders and cross references to fuller identificatory and ecological information appears in tabular form in the Appendix.

1.5 INSECTS IN POPULAR CULTURE AND COMMERCE

People have been attracted to the beauty or mystique of certain insects throughout time. We know the importance of scarab beetles to the Egyptians as religious items, but 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. Cicadas were regarded by the ancient Chinese as symbolizing rebirth or immortality. In Mesopotamian literature the *Poem of Gilgamesh* alludes to odonates (dragonflies/damselflies) as signifying the impossibility of immortality. For the San ("bushmen") of the Kalahari, the praying mantis carries much cultural symbolism, including creation and patience in zen-like waiting. Amongst the personal or clan totems of Aboriginal Australians of the Arrernte language groups are *yarumpa* (honey ants) and *udnirringitta* (witchety grubs). Although these insects are important as food in the arid central Australian environment (see section 1.6.1), they 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 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 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.

Urbanized humans have lost much of this contact with insects, excepting those that share our domicile, such as cockroaches, tramp ants, and hearth crickets which generally arouse antipathy. Nonetheless, specialized 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. Natural occurrences of certain insects attract ecotourism, including aggregations of overwintering monarch butterflies in coastal central California (see Plate 3.5) and Mexico, the famous glow worm caves of Waitomo, New Zealand, and Costa Rican locations such as Selva Verde representing tropical insect biodiversity.

Although insect ecotourism may be in its infancy, other economic benefits are associated with interest in insects. This is especially so amongst children in

Japan, where native rhinoceros beetles (Scarabaeidae, *Allomyrina dichotoma*) sell for US$3–7 each, and longer-lived common stag beetles for some US$10, and may be purchased from automatic vending machines. Adults collect too with a passion: a 7.5 cm example of the largest Japanese stag beetles (Lucanidae, *Dorcus curvidens*, called *o-kuwagata*) may 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 reared, have fetched several million yen (>US$10,000) at the height of the craze. 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 south and south-east Asia. Enthusiasm for valuable specimens extends outside Coleoptera: Japanese and German tourists are reported to buy rare butterflies in Vietnam for US$1000–2000, which is a huge sum of money for the generally poor local people.

Entomological revenue can enter local communities and assist in natural habitat conservation when tropical species are reared for living butterfly exhibits in the affluent world. An estimated 4000 species of butterflies have been reared in the tropics and exhibited live in butterfly houses in North America, Europe, Malaysia, and Australia. Farming butterflies for export is a successful economic activity in Costa Rica, Kenya, and Papua New Guinea. Eggs or wild-caught larvae are reared on appropriate host plants, grown until pupation, and freighted by air to butterfly farms. Papilionidae, including the well-known swallowtails, graphiums, and birdwings, are most popular, but research into breeding requirements allows an expanded range of potential exhibits to be located, reared, and shipped. In East Africa, the National Museums of Kenya has combined with local people of the Arabuko-Sukoke forest in the Kipepeo Project to export harvested butterflies for live overseas exhibit, thereby providing a cash income for these otherwise impoverished people.

In Asia, particularly in Malaysia, there is interest in rearing, exhibiting, and trading in mantises (Mantodea), including orchid mantises (*Hymenopus* species; see pp. 329 and 358) 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 concerning whether wild insect collection, either for personal interest or commercial trade and display, is sustainable. Much butterfly, dragonfly, stick-insect, and beetle trade relies more on collections from the wild than rearing programs, although this is changing as regulations increase and research into rearing techniques continues. In the Kenyan Kipepeo Project, although specimens of preferred lepidopteran species originate from the wild as eggs or early larvae, walk-through visual assessment of adult butterflies in flight suggested that the relative abundance rankings of species was unaffected regardless of many years of selective harvest for export. Furthermore, local appreciation has increased for intact forest as a valuable resource rather than viewing it as "wasted" land to clear for subsistence agriculture. 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 INSECTS AS FOOD

1.6.1 Insects as human food: entomophagy

In this section we review the increasingly popular study of insects as human food. Probably 1000 or more species of insects in more than 370 genera and 90 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. 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 mollusks are favored culinary items. Objections to eating insects cannot be justified on the grounds of taste or food value. Many have a nutty flavor and studies report favorably on the nutritional content of insects,

Table 1.2 Proximate, mineral, and vitamin analyses of four edible Angolan insects (percentages of daily human dietary requirements/100 g of insects consumed). (After Santos Oliviera et al. 1976, as adapted by DeFoliart 1989.)

Nutrient	Requirement per capita (reference person)	*Macrotermes subhyalinus* (Termitidae)	*Imbrasia ertli* (Saturniidae)	*Usta terpsichore* (Saturniidae)	*Rhynchophorus phoenicus* (Curculionidae)
Energy	2850 kcal	21.5%	13.2%	13.0%	19.7%
Protein	37 g	38.4	26.3	76.3	18.1
Calcium	1 g	4.0	5.0	35.5	18.6
Phosphorus	1 g	43.8	54.6	69.5	31.4
Magnesium	400 mg	104.2	57.8	13.5	7.5
Iron	18 mg	41.7	10.6	197.2	72.8
Copper	2 mg	680.0	70.0	120.0	70.0
Zinc	15 mg	–	–	153.3	158.0
Thiamine	1.5 mg	8.7	–	244.7	201.3
Riboflavin	1.7 mg	67.4	–	112.2	131.7
Niacin	20 mg	47.7	–	26.0	38.9

although their amino acid composition needs to be balanced with suitable plant protein. Nutritional values obtained from analyses conducted on samples of four species of insects cooked according to traditional methods in central Angola, Africa are shown in Table 1.2. The insects concerned are: reproductive individuals of a termite, *Macrotermes subhyalinus* (Isoptera: Termitidae), which are de-winged and fried in palm oil; the large caterpillars of two species of moth, *Imbrasia ertli* and *Usta terpsichore* (Lepidoptera: Saturniidae), which are de-gutted and either cooked in water, roasted, or sun-dried; and the larvae of the palm weevil, *Rhynchophorus phoenicis* (Coleoptera: Curculionidae), which are slit open and then fried whole in oil.

Mature larvae of *Rhynchophorus* species have been appreciated by people in tropical areas of Africa, Asia, and the Neotropics for centuries. These fat, legless grubs (Fig. 1.2), often called palmworms, provide one of the richest sources of animal fat, with substantial amounts of riboflavin, thiamine, zinc, and iron (Table 1.2). Primitive cultivation systems, involving the cutting down of palm trees to provide suitable food for the weevils, are known from Brazil, Colombia, Paraguay, and Venezuela. In plantations, however, palmworms are regarded as pests because of the damage they can inflict on coconut and oil palm trees.

In central Africa, the people of southern Zaire (presently Democratic Republic of Congo) eat caterpillars belonging to 20–30 species. The calorific value of these
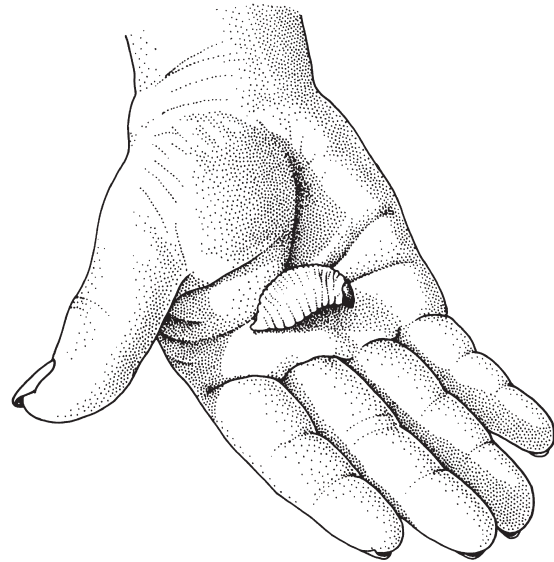
Fig. 1.2 A mature larva of the palm weevil, *Rhynchophorus phoenicis* (Coleoptera: Curculionidae) – a traditional food item in central Angola, Africa. (Larva after Santos Oliveira et al. 1976.)

caterpillars is high, with their protein content ranging from 45 to 80%, and they are a rich source of iron. For instance, caterpillars are the most important source of animal protein in some areas of the Northern Province

of Zambia. The edible caterpillars of species of *Imbrasia* (Saturniidae), an emperor moth, locally called mumpa, provide a valuable market. The caterpillars contain 60–70% protein on a dry-matter basis and offset malnutrition caused by protein deficiency. Mumpa are fried fresh or boiled and sun-dried prior to storage. Further south in Africa, *Imbrasia belina* moth (see Plate 1.4) caterpillars (see Plate 1.5), called mopane, mopanie, mophane, or phane, are utilized widely. Caterpillars usually are de-gutted, boiled, sometimes salted, and dried. After processing they contain about 50% protein and 15% fat – approximately twice the values for cooked beef. Concerns that harvest of mopane may be unsustainable and over-exploited are discussed under conservation in Box 1.3.

In the Philippines, June beetles (melolonthine scarabs), weaver ants (*Oecophylla smaragdina*), mole crickets, 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 consumed. Harvesting involved driving grasshoppers into a pit in the ground by 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) are called witchety grubs from an 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, 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 estivating sites in narrow caves and crevices on mountain summits in south-eastern 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 2.3). These galls occur only on bloodwood
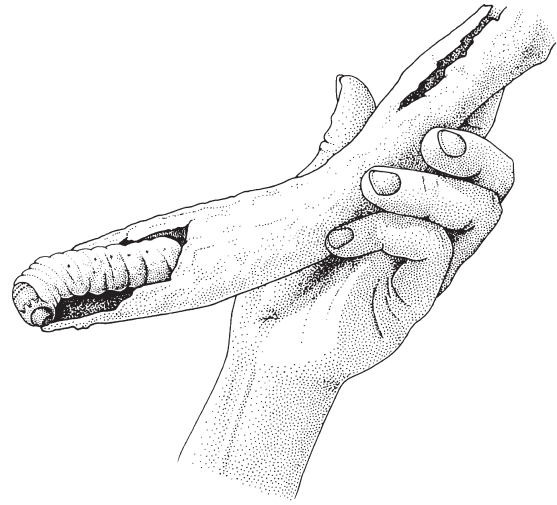
Fig. 1.3 A delicacy of the Australian Aborigines – a witchety (or witjuti) grub, a caterpillar of a wood moth (Lepidoptera: Cossidae) that feeds on the roots and stems of witjuti bushes (certain *Acacia* species). (After Cherikoff & Isaacs 1989.)

eucalypts (*Corymbia* species) and can be very abundant after a favorable growing season. Each mature gall 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 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 (see Plate 2.4). Aborigines relish the watery female insect and her nutty-flavored nymphs, then scrape out and consume the white coconut-like flesh of the inner gall.

A favorite source of sugar for Australian Aboriginals living in arid regions comes from species of *Melophorus* and *Camponotus* (Formicidae), popularly known as honeypot ants. Specialized workers (called repletes) store nectar, fed to them by other workers, in their huge distended crops (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 from their underground nests, an activity most frequently undertaken by women, who may excavate pits to a depth of a meter 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 USA and Mexico belong to a dif-

ferent 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 to counter a popular conception 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 2.1). 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* (see Plate 1.6) or the Thai and Laotian *mangda* sauces made with the flavors extracted from the male abdominal glands, for which high prices are paid. Even in the urban USA some insects may yet become popular as a food novelty. The millions of 17-year cicadas that periodically plague cities like Chicago 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 favorite 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 colored insects are often distasteful or toxic (Chapter 14) and some people can develop allergies to insect material (section 15.2.3). 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 programs, 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.

1.6.2 Insects as feed for domesticated animals

If you do not relish the prospect of eating insects yourself, then perhaps the concept of insects as a protein source for domesticated animals is more 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 fish meal diets. The insects involved are primarily the pupae of silkworms (*Bombyx mori*) (see Plate 2.1), 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, can be used as 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 the development of a range of insect recycling systems for converting organic wastes into feed supplements is inevitable, given that most organic substances are fed on by one or more insect species.

Clearly, insects can 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 needs, 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.

1.7 INSECT CONSERVATION

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. 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 increases the number and size of areas to conserve many insects, which are not (and arguably "do not need to be") understood on a species-by-species approach. 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 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. 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, 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. Monarchs from east of the Rockies overwinter in Mexico and 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 in Mexico. A most significant insect conservation measure implemented in recent years is the decision of the Mexican government to support the Monarch Butterfly Biosphere Reserve established to protect the phenomenon. Although the monarch butterfly is an excellent flagship

insect, the preservation of western overwintering populations in coastal California (see Plate 3.5) protects 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 are faunistically depauperate in their non-native habitat.

A successful example of single-species conservation involves the El Segundo blue, *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 interests 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 (PNG) is a success story from the developing world. This spectacular species, whose caterpillars feed only on *Aristolochia dielsiana* vines, is limited to a small area of lowland rainforest in northern PNG and has been listed as endangered. Under PNG law, this birdwing species has been protected since 1966, and international commercial trade was banned by listing on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Dead specimens in good condition command a high price, which can be more than US$2000. In 1978, the PNG governmental Insect Farming and Trading Agency (IFTA), in Bulolo, Morobe Province, was established to control conservation and exploitation and act as a clearing-house for trade in Queen Alexandra's birdwings and other valuable butterflies. Local cultivators, numbering some 450 village farmers associated with IFTA, "ranch" their butterflies. In contrast to the Kenyan system described in section 1.5, farmers plant appropriate host vines, often on land already cleared for vegetable gardens at the forest edge, thereby providing food plants for a chosen local species of butterfly. Wild adult butterflies emerge from the forest to feed and lay their eggs; hatched larvae feed on the vines until pupation when they are collected and protected in hatching cages. According to species, the purpose for which they

are being raised, and conservation legislation, butterflies can be exported live as pupae, or dead as high-quality collector specimens. IFTA, a non-profit organization, sells some $400,000 worth of PNG insects yearly to collectors, scientists, and artists around the world, generating an income for a society that struggles for cash. As in Kenya, local people recognize the importance of maintaining intact forests as the source of the parental wild-flying butterflies of their ranched stock. In this system, the Queen Alexandra's birdwing butterfly has acted as a flagship species for conservation in PNG and the success story attracts external funding for surveys and reserve establishment. In addition, conserving PNG forests for this and related birdwings undoubtedly results in conservation of much diversity under the umbrella effect.

The Kenyan and New Guinean insect conservation efforts have a commercial incentive, providing impoverished people with some recompense for protecting natural environments. Commerce need not be the sole motivation: the aesthetic appeal of having native birdwing butterflies flying wild in local neighborhoods, combined with local education programs in schools and communities, has saved the subtropical Australian Richmond birdwing butterfly (*Troides* or *Ornithoptera richmondia*) (see Plate 2.2). Larval Richmond birdwings eat *Pararistolochia* or *Aristolochia* vines, choosing from three native species to complete their development. However, much 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, has been luring females to lay eggs on it as a prospective host. This oviposition mistake is deadly since toxins of this plant kill young caterpillars. The answer to this conservation problem has been an education program to encourage the removal of Dutchman's pipe vines from native vegetation, from sale in nurseries, and from gardens and yards. Replacement with native *Pararistolochia* was encouraged after a massive effort to propagate the vines. Community action throughout the native range

of the Richmond birdwing appears to have reversed its decline, without any requirement to designate land as a reserve.

Evidently, butterflies are flagships for invertebrate conservation – they are familiar insects with a non-threatening lifestyle. However, certain orthopterans, including New Zealand wetas, have been afforded protection, and we are aware also of conservation plans for dragonflies and other freshwater insects in the context of conservation and management of aquatic environments, and of 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) includes perhaps 50% of the butterfly diversity of some 6000 species. Many have relationships with ants (myrmecophily; see 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 tended by ants. These relationships can be very complex, and may be rather easily disrupted by environmental changes, leading to endangerment of the butterfly. Certainly in western Europe, species of Lycaenidae figure prominently on lists of threatened insect taxa. Notoriously, the decline of the large blue butterfly *Maculinea arion* in England was blamed upon overcollection and certainly some species have been sought after by collectors (but see Box 1.1). Action plans in Europe for the reintroduction of this and related species and appropriate conservation management of other *Maculinea* 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.

Box 1.1 Collected to extinction?

The large blue butterfly (*Maculinea arion*) 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 south-western England. Only one or two 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 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 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 been revealed by research associated with 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 behavior, and/or tricking ants into feeding them as if they were the ants' own brood, are features
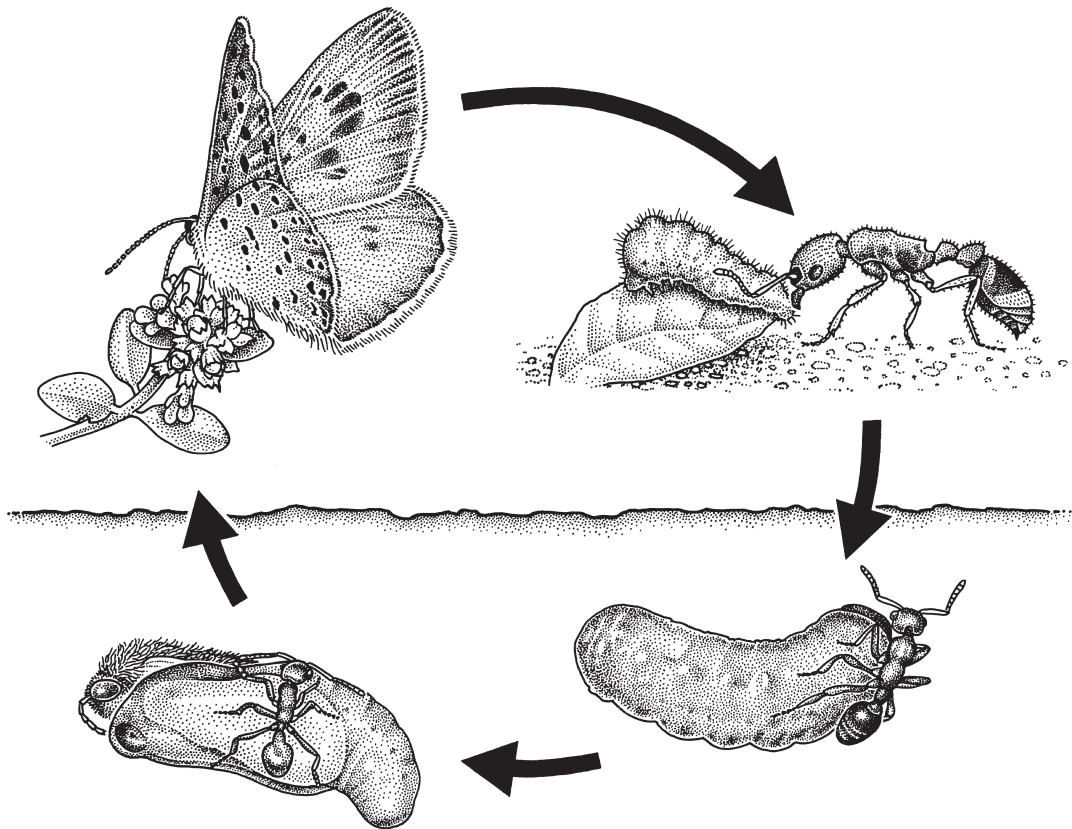
in the natural history of many Lycaenidae (blues and coppers) worldwide (see p. 15). After hatching from an egg laid on the larval food plant, the large blue's caterpillar feeds on thyme flowers until the molt into the final (fourth) larval instar, around August. At dusk, the caterpillar drops to the 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 brood and grows for 9 months until it pupates in early summer of the following year. The caterpillar requires an average 230 immature ants for successful pupation. 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 favoring other *Myrmica* species, including *M. scabrinodes* that 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 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 the caterpillar becomes imbued with the chemical odors of queen larvae while feeding and, with numerous alate queens in the nest, 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 vegetational 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 climate change on a broader scale must play a role. 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 an umbrella role for the butterfly species.

Box 1.2 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 century. In fact all social insects (honey bees, yellowjackets, paper wasps, termites, and ants) on Hawai'i arrived with 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 behavioral subset 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 megaceph-*

ala), the long legged or yellow crazy ant (*Anoplolepis longipes*), the Argentine ant (*Linepithema humile*), the "electric" or little fire ant (*Wasmannia auropunctata*), and tropical fire ants (*Solenopsis* species) are considered the most serious of these ant pests.

Invasive ant behavior threatens biodiversity, especially on islands such as Hawai'i, the Galapagos and other Pacific Islands (see 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. Tramp ants' tendency to be small and short-lived is compensated by year-round increase and rapid production of new queens. Nestmate queens show no hostility to each other. Colonies reproduce by the mated queen and workers relocating only a short distance from the original nest – a process known as budding. When combined with the absence of intra-specific antagonism between newly founded and natal nests, colony budding ensures the gradual spreading of a "supercolony" across the ground.

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 unim-pacted control sites, but the arrival of *P. megacephala* dramatically restructured the system, seriously reduc-ing 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 south-eastern USA, and ground-nesting birds every-where. 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 which carry smaller seeds (see 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.
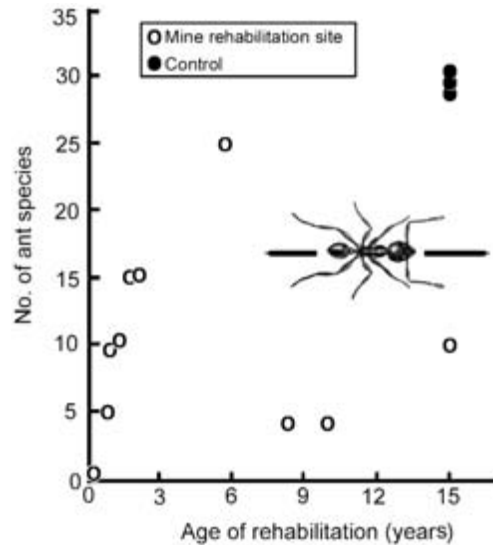
Introduced ants are very difficult to eradicate: all attempts to eliminate fire ants in the USA have failed. We will see if an A\$123 million (\$US50 million), five-year campaign to rid Australia of *Solenopsis invicta* will prevent it from establishing as an "invasive" species. The first fire ant sites were found around Brisbane in February 2001, and two years later the peri-urban area under surveillance for fire ants extended to some 47,000 ha. Potential economic damage in excess of A\$100 billion over the next 30 years is estimated if control fails, with inestimable damage to native biodivers-ity continent-wide. Although intensive searching and destruction of nests appears to be successful, all must be eradicated to prevent resurgence. Undoubtedly the best strategy for control of invasive ants is quarantine diligence to prevent their entry, and public awareness to detect accidental entry.

Box 1.3 Sustainable use of mopane worms

An important economic insect in Africa is the larva (caterpillar) of emperor moths, especially *Imbrasia belina* (see Plates 1.4 & 1.5, facing p. 14), which is harvested for food across much of southern Africa, including Angola, Namibia, Zimbabwe, Botswana, and Northern Province of South Africa. The distribution coincides with that of mopane (*Colophospermum mopane*), a leguminous tree which is the preferred host plant of the caterpillar and dominates the "mopane woodland" landscape.

Early-instar larvae are gregarious and forage in aggregations of up to 200 individuals: individual trees may be defoliated by large numbers of caterpillars, but regain their foliage if seasonal rains are timely. Throughout their range, and especially during the first larval flush in December, mopane worms are a valued protein source to frequently protein-deprived rural populations. A second cohort may appear some 3–4 months later if conditions for mopane trees are suitable. It is the final-instar larva that is harvested, usually by shaking the tree or by direct collecting from foliage. Preparation is by degutting and drying, and the product may be canned and stored, or transported for sale to a developing gastronomic market in South African towns. Harvesting mopane produces a cash input into rural economies – a calculation in the mid-1990s suggested that a month of harvesting mopane generated the equivalent to the remainder of the year's income to a South African laborer. Not surprisingly, large-scale organized harvesting has entered the scene accompanied by claims of reduction in harvest through unsustainable over-collection. Closure of at least one canning plant was blamed on shortfall of mopane worms.

Decline in the abundance of caterpillars is said to result from both increasing exploitation and reduction in mopane woodlands. In parts of Botswana, heavy commercial harvesting is claimed to have reduced moth numbers. Threats to mopane worm abundance include deforestation of mopane woodland and felling or branch-lopping to enable caterpillars in the canopy to be brought within reach. Inaccessible parts of the tallest trees, where mopane worm density may be highest, undoubtedly act as refuges from harvest and provide the breeding stock for the next season, but mopane trees are felled for their mopane crop. However, since mopane trees dominate huge areas, for example over 80% of the trees in Etosha National Park are mopane, the trees themselves are not endangered.

The problem with blaming the more intensive harvesting for reduction in yield for local people is that the species is patchy in distribution and highly eruptive. The years of reduced mopane harvest seem to be associated with climate-induced drought (the El Niño effect) throughout much of the mopane woodlands. Even in Northern Province of South Africa, long considered to be over-harvested, the resumption of seasonal, drought-breaking rains can induce large mopane worm outbreaks. This is not to deny the importance of research into potential over-harvesting of mopane, but evidently further study and careful data interpretation are needed.

Research already undertaken has provided some fascinating insights. Mopane woodlands are prime elephant habitat, and by all understanding these megaherbivores that uproot and feed on complete mopane trees are keystone species in this system. However, calculations of the impact of mopane worms as herbivores showed that in their six week larval cycle the caterpillars could consume 10 times more mopane leaf material per unit area than could elephants over 12 months. Furthermore, in the same period 3.8 times more fecal matter was produced by mopane worms than by elephants.

Elephants notoriously damage trees, but this benefits certain insects: the heartwood of a damaged tree is exposed as food for termites providing eventually a living but hollow tree. Native bees use the resin that flows from elephant-damaged bark for their nests. Ants nest in these hollow trees and may protect the tree from herbivores, both animal and mopane worm. Elephant populations and mopane worm outbreaks vary in space and time, depending on many interacting biotic and abiotic factors, of which harvest by humans is but one.

FURTHER READING

Berenbaum, M.R. (1995) *Bugs in the System. Insects and their Impact on Human Affairs.* Helix Books, Addison-Wesley, Reading, MA.

Bossart, J.L. & Carlton, C.E. (2002) Insect conservation in America. *American Entomologist* **40**(2), 82–91.

Collins, N.M. & Thomas, J.A. (eds.) (1991) *Conservation of Insects and their Habitats.* Academic Press, London.

DeFoliart, G.R. (ed.) (1988–1995) *The Food Insects Newsletter.* Department of Entomology, University of Wisconsin, Madison, WI. [See Dunkel reference below.]

DeFoliart, G.R. (1989) The human use of insects as food and as animal feed. *Bulletin of the Entomological Society of America* **35**, 22–35.

DeFoliart, G.R. (1995) Edible insects as minilivestock. *Biodiversity and Conservation* **4**, 306–21.

DeFoliart, G.R. (1999) Insects as food; why the western attitude is important. *Annual Review of Entomology* **44**, 21–50.

Dunkel, F.V. (ed.) (1995–present) *The Food Insects Newsletter.* Department of Entomology, Montana State University, Bozeman, MT.

Erwin, T.L. (1982) Tropical forests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin* **36**, 74–5.

Gaston, K.J. (1994) Spatial patterns of species description: how is our knowledge of the global insect fauna growing? *Biological Conservation* **67**, 37–40.

Gaston, K.J. (ed.) (1996) *Biodiversity. A Biology of Numbers and Difference.* Blackwell Science, Oxford.

Gaston, K.J. & Hudson, E. (1994) Regional patterns of diversity and estimates of global insect species richness. *Biodiversity and Conservation* **3**, 493–500.

Hammond, P.M. (1994) Practical approaches to the estimation of the extent of biodiversity in speciose groups. *Philosophical Transactions of the Royal Society, London B* **345**, 119–36.

International Commission of Zoological Nomenclature (1985) *International Code of Zoological Nomenclature*, 3rd edn. International Trust for Zoological Nomenclature, London, in association with British Museum (Natural History) and University of California Press, Berkeley, CA.

May, R.M. (1994) Conceptual aspects of the quantification of the extent of biodiversity. *Philosophical Transactions of the Royal Society, London B* **345**, 13–20.

New, T.R. (1995) *An Introduction to Invertebrate Conservation Biology*. Oxford University Press, Oxford.

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. & Drozi, P. (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature* **416**, 841–4.

Price, P.W. (1997) *Insect Ecology*, 3rd edn. John Wiley & Sons, New York.

Roberts, C. (1998) Long-term costs of the mopane worm harvest. *Oryx* **32**(1), 6–8.

Samways, M.J. (1994) *Insect Conservation Biology*. Chapman & Hall, London.

Speight, M.R., Hunter, M.D. & Watt, A.D. (1999) *Ecology of Insects. Concepts and Applications*. Blackwell Science, Oxford.

Stork, N.E. (1988) Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society* **35**, 321–37.

Stork, N.E. (1993) How many species are there? *Biodiversity and Conservation* **2**, 215–32.

Stork, N.E., Adis, J. & Didham, R.K. (eds.) (1997) *Canopy Arthropods*. Chapman & Hall, London.

Tsutsui, N.D. & Suarez, A.V. (2003) The colony structure and population biology of invasive ants. *Conservation Biology* **17**, 48–58.

Vane-Wright, R.I. (1991) Why not eat insects? *Bulletin of Entomological Research* **81**, 1–4.

Wheeler, Q.D. (1990) Insect diversity and cladistic constraints. *Annals of the Entomological Society of America* **83**, 1031–47.

See also articles in "Conservation Special" *Antenna* **25**(1) (2001) and "Arthropod Diversity and Conservation in Southern Africa" *African Entomology* **10**(1) (2002).