

# Lepidoptera and Invertebrate Conservation

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## Introduction

Lepidoptera, the butterflies and moths, have for long been familiar both to naturalists and people in many other walks of life. Butterflies, arguably the most popular of all insect groups, have been a major focus for collectors and other hobbyists, as symbols of the wealth and health of the ecosystems that support them – and those interests have also contributed to concerns arising from their declines and, in a few cases, well publicised extinctions. The clearly documented losses of taxa such as the Large copper (*Lycaena dispar dispar*) from the fens of eastern England in the mid nineteenth century (Duffey 1977, Feltwell 1995) and reported decline of the Xerces blue (*Glaucopsyche xerces*) a decade or so later in the western United States (where it became extinct later: Pyle 2012), for example, each mark the beginnings of concern for insect conservation in those regions. More widely, the popularity of butterflies and later extinctions (such as of yet another lycaenid, the Large blue, *Maculinea arion*, in Britain as recently as 1979: Thomas 1991) have led to studies on these insects forming the strongest foundation of the developing science of insect conservation. Several factors contribute to this – simple aesthetics are important in creating a liking and sympathy for conspicuous insects, whether they are tiny lycaenids, as the above cases, or large and spectacular tropical swallowtails or birdwings (Papilionidae) such as those that enthralled explorers of then remote parts of the world during the Victorian era, and continue to do so. That era saw the proliferation of natural history documentation, prompted in part through the ‘philatelic approach’ to collecting, with progressive accumulation of distribution records, biological and life history details. These interests induced production of increasingly complete and sophisticated illustrated handbooks that enabled hobbyists to identify their study objects with reasonable certainty and summarise biological

and distributional information, and so to confidently contribute further to the record of fact and inference that has provided a vital legacy to present-day students. This legacy is geographically biased, of course, but the 200 years and more of accumulated information has rendered the butterflies of Britain, followed by those of some other parts of the northern temperate zones, the best documented of all regional insect faunas. In short, they are informative as examples and models for emulation and understanding to biologists seeking a foothold in the daunting world of invertebrate diversity. Importantly, they are accessible to non-specialists, encouraged by the wealth of well illustrated identification guides and authoritative but non-technical information available.

Butterflies are unusual, also, in their cultural connotations, with artistic roles since pre-Columbian years (Pogue 2009) including representation in the ancient art from many parts of the world, as well as presence in literature, myth and religion – the latter including symbolised connection to the soul in several distinct cultures. That, in general, people ‘like butterflies’ and do not fear them as harmful renders them popular and powerful ambassadors for the wealth of insect life. However, there is also suggestion that the appeal of such insects may link to ‘academic disapproval’ and deter young scientists from taking up study of the group. Study of such aesthetically pleasing insects is occasionally associated with second-rate intellect, so that supervisors may lead potential lepidopterist graduate students to turn their focus to ‘insect taxa that are judged to be more academically respectable’ (Kristensen et al. 2007). Simplistically, butterflies, together with a few families of larger showy moths (notably hawkmoths, Sphingidae, and silk moths, Saturniidae) and the brightly coloured day-active burnets (Zygaenidae), are commonly regarded as ‘beginners’ bugs’, simply because they are attractive and accessible easily by non-specialists. The reality is far different, as much recent literature – some cited in later chapters – demonstrates!

However, the butterflies are only a small component of one of the largest insect orders. They comprise only some 20,000 named species, a total surpassed by each of several individual families of moths which comprise, perhaps, a further 350,000 species. Powell (2003) estimated global Lepidoptera species richness as ‘certain to exceed 350,000 species’ with considerable uncertainty over what the real total may be, and rather more than 160,000 species having been named. These are distributed amongst about 124 families grouped into 47 superfamilies (Kristensen 1999). More recently, and incorporating the uncertainty implied here, Kristensen et al. (2007) estimated that ‘There are considerably more than a quarter-million Lepidoptera species, probably in the order of magnitude of half a million, but there are not a million – let alone several millions’. The theme of taxonomic diversity is revisited in Chapter 2, and is noted here simply to emphasise that we are dealing with an enormous group of insects – confidently amongst the four largest orders of insects as they are at present understood, and probably the smallest of the four – and amongst which biological and taxonomic knowledge is very uneven (Scoble 1992). Estimates of species numbers are difficult, not least because of the great variety of species concepts used in modern biology, and the transition from simple morphospecies to greater appreciation of intrinsic variation may affect the number of entities recognised very considerably.

Our confidence from studies on butterflies dissipates rapidly when confronted with our ignorance over many moths. The ‘accessibility’ of butterflies contrasts markedly with the confusions that flow from many small moths, and is coupled also with the very different image many people have of moths, as annoying, drab, nocturnal pests: each a sweeping generalisation to which there are many exceptions! The masterly introductory chapter to ‘Moths’ (Majerus 2002) gives much background to this dichotomy of perceptions. Progressive incorporation of moths to augment the conservation perspective founded in butterflies (Chapter 4) is enriching the themes underpinning much insect conservation and enlarging appreciation of the biological templates against which insect diversity can be appraised. Majerus (2002) ventured that, for Britain, the strong faunistic knowledge has rendered Lepidoptera the most suitable group for studying the impacts of anthropogenic changes on terrestrial fauna. Many others have expressed similar confidence.

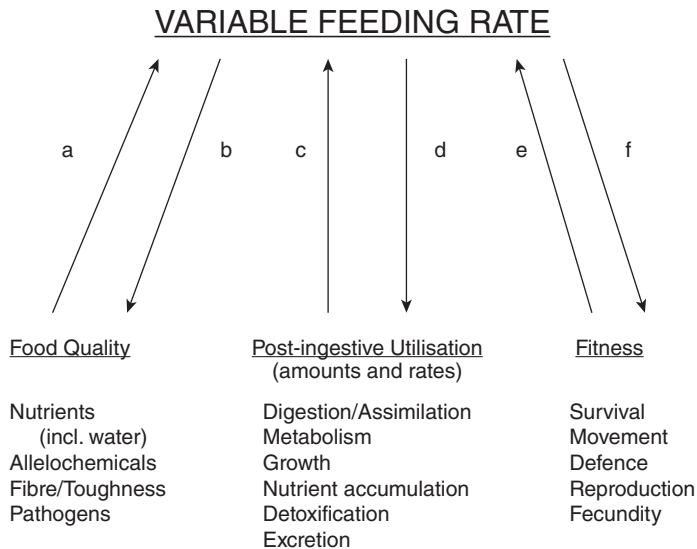
## **Biological background**

Lepidoptera are not an ancient order. Unlike the Coleoptera, accepted widely as the most diverse of all insect orders and which occur in the fossil record from the Permian era some 250 million years ago, Lepidoptera proliferated only in the Cretaceous period, developing and radiating in parallel with the flowering plants and so broadly ‘only’ about 100 million years old. The fossil record is very sparse: Kristensen and Skalski (1999) estimated that only 600–700 specimens of fossil Lepidoptera were then known, a high proportion of them in resins, and including Baltic amber as a major source. Although some fossils believed to be Lepidoptera occur nearly 200 million years ago in the Jurassic, the major lineages of the order seemingly developed much more recently. Details will continue to be refined as further evidence accumulates, as will how angiosperm development really fostered diversification of Lepidoptera (Powell 2009). However, the Lepidoptera constitutes perhaps the largest single evolutionary lineage adapted to depend on living plants (Powell & Opler 2009).

Those early coevolutions with angiosperms apparently founded the two major ecological roles associated with modern Lepidoptera. Many adult Lepidoptera feed on plant nectar, and collectively display a range of features that render many of them effective, and sometimes highly specific, pollinators. Larvae, caterpillars, of most Lepidoptera are chewing herbivores and, whilst most feed on or in foliage, particular taxa may exploit virtually any part of a plant. Lepidoptera are widely considered the most important insect group of defoliators. Many species are very specialised in feeding habit, and strict host plant specificity is common; that specificity may extend from plant taxon to tissue, growth stage, season, degree of exposure (sun or shade environments) and many other restrictions that may influence resource accessibility and suitability, and which must be considered in conservation management. The key realisation is simply that every species of Lepidoptera comprises two very different biological entities, with larva and adult disparate in form and habits; they occupy different habitats (commonly at different times of the year with little or no seasonal overlap) and

exploit different resources, so have different ecological pressures and needs for conservation. For many species, the larva, although less often observed, is the dominant stage, far longer lived than the relatively transient adult stage. In essence, the two stages are ‘twin’ organisms and the needs of both are central to conservation. Those needs include, as examples, how adults track nectar sources for food and find suitable oviposition sites, and how larvae find and exploit plant or (rarely) other foods, withstand depredations of predators and parasitoids and later find suitable pupation sites. Adults may need to disperse actively, sometimes over large distances as seasonal migrants, with most caterpillars in contrast dispersing rather little from where they eclose. Intricate behavioural cues and ecological strategies and specialisations are rife amongst Lepidoptera, and understanding and heeding these is another important component of conservation. Activity of both stages is influenced strongly by temperature and a range of other environmental features, as well as the accessibility of key foodstuffs – often very specific – that have led to highly characteristic seasonal and spatial patterns of development. Dispersion of the key resources (Chapter 7) from local to landscape scales is thus a critical aspect of conservation, with many of the trophic associations long entrenched over evolutionary time.

In common with many other insect herbivores, a particular obligatory food plant species may not always be suitable, but factors such as water or nitrogen content, exposure of the plant and presence of plant defensive chemicals influence local or seasonal exploitation. Figure 1.1 illustrates some of these constraints and, as Slansky (1993) commented, ‘For a caterpillar . . . feeding involves



**Fig. 1.1** Interactions between feeding rate and food quality, food utilisation and fitness in insect herbivores: (a) food quality can affect feeding rate, and (b) feeding may affect food quality; (c) post-ingestive food utilisation can affect feeding rate, and (d) the converse; (e) fitness components may affect feeding rate, and (f) feeding affects fitness (Source: Slansky 1993. Reproduced with permission of John Wiley & Sons.).

much more than merely filling its gut with the nearest available plant tissue'. However, it is commonplace for a suitable food plant species to be much more widely distributed than a specialist insect herbivore, and reasons for herbivore absence at places well within its range and dispersal capability are often anomalous. 'Host quality' factors affect plant suitability in time and space, and also influence incidence and abundance of the Lepidoptera (Dennis 2010).

Understanding these factors is critical in fine-scale conservation management, and their elucidation may involve very detailed study. The Sandhill rustic moth (*Luperina nickerlii leechi*, Noctuidae, Chapter 5, p. 51) is known only from one site in Cornwall, southern England, where caterpillars are associated with sand couch-grass (*Elytrigia juncea*). There are large areas on the site where the plant occurs but the moth does not (Spalding et al. 2012). *Luperina* is associated with abundant host plant cover and high numbers of stems and rhizomes – but is also restricted to areas with bare ground and levels of disturbance, so that the suitability of the host plants represents 'a fine balance between disturbance and vegetation condition'. Discussed in detail by Spalding et al. 2012, maintenance of suitable conditions involves attention to creating areas of bare ground with coarse shingle and extensive, vigorous patches of *Elytrigia*, and few other competing plants. Occasional disturbance may be beneficial, deterring establishment of competing vegetation.

Most present-day associations with host plant taxa are outcomes of long evolutionary associations (Powell et al. 1999), but many geographical gaps in knowledge persist, and much of the interpretation of host–plant relationships has arisen from northern temperate region studies. A key presumption in conservation is that natural associations involving native plants and native insects are the ideal target for sustainability. In other cases, however, alien plants (such as weeds or ornamentals) may be adopted as resources and add further, sometimes complex, dimensions to conservation management. Native Lepidoptera may 'switch' to utilise such alien hosts, which can become important components of the species' ecology – for example, as substitutes for natural hosts that have declined or been lost to development. Thus, in North America, the endangered Taylor's checkerspot butterfly (*Euphydryas editha taylori*, Nymphalidae) has switched, from unknown original native host(s), to becoming entirely dependent on the alien *Plantago lanceolata* (Severns & Warren 2008). The decline of *E. e. taylori*, to the extent that it was long believed to be extinct in Oregon, where it is now known from two sites (together with a possible one on Vancouver Island and one large and several small populations in Washington State), is attributed to impacts of invasive alien grasses and shrubs overgrowing and reducing abundance of native forb foodplants, with grasses also reducing access of butterflies to basking sites (Severns & Warren 2008). Control of alien grasses was seen as the key need to prevent the Oregon populations becoming extinct. In parallel the encouragement or, at least, tacit tolerance, of the alien *Plantago* is the only known key to sustaining the butterfly. Such adoption of a novel host plant can occur quite rapidly, as possible hosts become available through changed land use patterns. The classic example of *E. editha*, explored by Singer et al. (1993), showed two populations to have independently adopted such hosts: in one case of *Plantago lanceolata* introduced by cattle ranchers and in the other of *Collinsia*

*torreyi* appearing in clearcut patches created by logging. That some individual butterflies tested rejected their normal ancestral host in favour of the recently adventive species created a conservation scenario incorporating rapid genetic adaptation to human-induced changes, and perhaps dependence of rare species on continued availability of these novel hosts. Adoption of the introduced Chilean needle grass (*Nassella neesiana*) in Australia by the endemic Golden sun-moth (*Synemon plana*, discussed later in this chapter) is amongst other such contexts for which parallel experimental investigations to determine any changes in preference are yet to be made.

However, it is also suggested widely that new associations of ‘alien plant–native lepidopteran’ are not generally as beneficial as the original ‘native plant–native lepidopteran’ associations that are being replaced or compensated. Alien invasive plants may have varied adverse impacts on native Lepidoptera, falling broadly into three main categories: (1) competitive exclusion and elimination of native host and/or nectar resource plants; (2) negative impacts without direct loss of native hosts, such as the latter being overgrown, not detected so easily, or the alien plants being more attractive to ovipositing females but not as suitable in sustaining offspring; and (3) creating structural changes that modify microclimates and influence interaction, such as those between mutualistic caterpillars and ants. These are not always easy to discover or discern, but some are reasonably unambiguous. The introduced South American vine *Aristolochia littoralis* (more familiarly termed *A. elegans* in the region) in subtropical eastern Australia is super-attractive to females of the Richmond birdwing butterfly (*Ornithoptera richmondia*, Chapter 9, p. 173) and acts as a decoy inducing females to lay on it rather than on their native foodplant vine, *Pararistolochia praevenosa* (Sands et al. 1997). *Aristolochia elegans* foliage, however, is toxic to the hatchling caterpillars, so that they are condemned to death by such oviposition, and spread of this alien vine into native forests is a major threat to the butterfly.

The native grassland habitats of the Golden sun-moth (*Synemon plana*, Castniidae, Chapter 9, p. 174) in south-eastern Australia are invaded by the alien Chilean needle grass, *Nassella neesiana*, a declared noxious weed – a status that legally obliges eradication attempts wherever it occurs. Current strong inference that it may be an important alternative host for subterranean *S. plana* caterpillars on some sites on which native grass hosts have become scarce continues to be debated amidst the conservation controversies between protecting a critically endangered moth by assuring a valuable food source and eliminating this invasive weed (New 2012a). As for *Plantago* and Taylor’s checkerspot, discussed earlier, the practical dilemma of tolerating and, even, fostering an invasive alien food plant in order to conserve a notable lepidopteran species, will almost inevitably generate disagreements and strong opinion for or against any such action.

Whilst the full complexities of caterpillar foraging and nutritional ecology are beyond the scope of this account, a conservationist must be aware that many subtleties exist and may need to be considered carefully in optimising food supply in species management. More generally, both caterpillars and adult butterflies or moths have numerous constraints on their activity, imposed by the structure and condition of their environment, the spatial distribution of their resource needs, and complexities of interactions with other species, including



**Table 1.1** The variety of biological features amongst caterpillars, as exemplified through a broader survey of herbivorous insects by Damman (1993). Reproduced with permission of John Wiley & Sons.

<i>Characteristic</i>	<i>Categories</i>
Feeding behaviour	Leaf chewers; leaf tiers; leaf miners; gall makers; stem borers; seed predators; fruit borers; root feeders
Feeding position	External (exposed to natural enemies, not bound to any sort of shelter); internal (living inside plant tissue or surrounded by shelter)
Gregariousness	Solitary (larvae feed independently); gregarious (larvae feed in groups, at least during early instars)
Specialisation	Specialists (restricted to one plant family or, in extreme cases, one plant species); generalists (feed on more than one plant family) [terms used at different levels by different authors]
Growth form of food plant	Almost any plant material in terrestrial environments and, more rarely, shallow freshwater environments; every gradation from short-lived highly seasonal annuals to long-lived perennials, and herbaceous to woody

competitors. These needs differ between species and, even, different caterpillar instars – so that, for example, fast growth may enable large size to be attained and be a refuge from natural enemies, or create resistance to some plant defences, or proffer competitive advantage over competing herbivores. Many different lifestyles occur among Lepidoptera (Table 1.1), and each represents a compromise between various ecological pressures (Damman 1993) to dictate a balance that must be sustained for the species to persist. The adaptations of many caterpillars are influenced strongly by the variety, distribution, condition and nutritional state of plant or other foods, and also by the influences of natural enemies, predators and parasitoids. As counters to these, many caterpillars have evolved to become cryptic (reducing detection), aposematic (advertising distastefulness and often exploiting plant chemicals to do so) or evolving physical (toughness, hairiness) barriers to attack or activity patterns that reduce exposure: ‘enemy-free space’ is itself a critical resource for many herbivorous insects. Any such lifestyle may be influenced or disrupted by competing species within the same milieu – so that, in addition to native species, introductions of alien plants, herbivores or higher-level carnivores (such as classical biological control agents, Chapter 12) may affect long-evolved balances between such naturally occurring trophic groups. Many such introductions are potential threats to native species. Two long-recognised forms of competition may occur, again discussed by Damman (1993): exploitation, in which the species involved compete directly for shared resources, here mainly for the same food plant species or tissues; and interference, in which access to a resource by one species necessitates actively excluding others (such as by aggressive behaviour or territoriality) or

in which the species continually impede each others' efforts to forage at the same time. Richmond birdwing caterpillars, discussed earlier in this chapter, are cannibalistic, a habit perhaps of considerable value in reducing competition for food on vines with relatively small amounts of foliage (Sands & New 2013) – each caterpillar of this large butterfly needs to eat about a square metre of leaves during its development! Much of the intricate behaviour of caterpillars may have evolved to reduce competition, facilitate access to food, or to avoid attacks by natural enemies. Nocturnal activity, for example, has an appealingly simplistic function, far more difficult to prove, of avoiding diurnally active predators and parasitoids. Another frequent development has been for caterpillars to become endophytic, occupying leaf mines, galls, stems or roots, in addition to others that make shelters or retreats of various kinds, such as by tying leaves together.

Most Lepidoptera are terrestrial, but caterpillars of a few – notably amongst some pyralid moths, Nymphulinae, feed on aquatic plants in fresh water environments. Herbivory (perhaps ancestrally on lower plants such as bryophytes – a habit that persists in some primitive moth lineages, but now mostly on angiosperms), although the predominant larval feeding habit, is not quite universal, with various forms of aphytophagy involving predation and feeding on exudates of Homoptera or ants having arisen independently in several lineages (see Hinton 1951, Cottrell 1984, Pierce 1995 for background) adding to the spectrum of ecological associations within the order. Whilst the vast majority of Lepidoptera (>99%: Common 1990) are herbivores, a complex and varied array of other larval feeding habits also occur, and these have defied attempts at easy categorisation (such as Hinton's (1951) 'biological groups' based on feeding habits) because of numerous intergrading levels. Pierce (1995) regarded Lepidoptera as 'remarkably unadventurous' as predators, with limited prey range and feeding methods; prey are almost always of arthropods (largely Homoptera or ants) which are sedentary or found near the caterpillars' food plants. Myrmecophily has arisen independently on a number of occasions (in at least eight lineages of lycaenids alone, for example: Cottrell 1984), and now involves many subtle and obligate mutualisms, with those within the Lycaenidae most intensively investigated (Pierce et al. 2002) and of considerable importance in conservation management. Thus, the dependence of large blue butterflies (*Maculinea*) on particular ant species, with caterpillars feeding on ant brood, is a key element in conservation management (Chapter 7, p. 127). At one extreme within the Lycaenidae, the subfamily Miletinae appear to be entirely carnivorous on ants. Both predation and cannibalism have developed repeatedly in different groups of Lepidoptera, with cannibalism perhaps a more widespread opportunistic response to food shortage in some taxa. Predation may become highly focused, with particular species of prey, whether Homoptera or ants, necessary. Some Australian species of *Stathmopoda* (Oecophoridae: Stathmopodinae) are specific predators on *Eriococcus* scale insects on eucalypts (*S. melanochra*) or spider egg-sacs (*S. arachnophora*); and the few species of Epipyropidae and Cyclotornidae (both Zygaenoidea) are ectoparasites of leafhoppers. *Cyclotorna monocentra* (an Australian endemic) lays eggs on trees infested with eurymelid leafhoppers (Dodd 1912), but the later instars are carried into ant



nests where they feed on ant larvae. Obligatory predators or parasites occur in eight superfamilies of Lepidoptera, in most of them only very sporadically. However, a few such cases have captured wide interest. The unique 'ambush' by caterpillars of *Eupithecia* species (Geometridae) in Hawaii involves them feeding only on live-caught insects and spiders that venture within range (Montgomery 1982), and depends on tactile stimuli as these possible prey contact caterpillars on vegetation. In common with numerous other endemic Hawaiian Lepidoptera, and as Montgomery foreshadowed, detailed study of this unusual adaptation may be thwarted by loss of the taxa as native ecosystems continue to be lost or invaded by alien taxa.

In some taxa, feeding habit changes markedly as larvae develop; some lycaenid butterfly caterpillars are initially phytophagous, but grow only slightly until they later switch to feeding on ant brood (*Maculinea arion*: Thomas 1989); less specifically, caterpillars of some Swift moths (Hepialidae) are initially detritivores or mycovores, but later feed on or in living plants (Grehan 1989). Such changes add further complexity to resource needs in conservation. As with strictly herbivorous taxa, any such relationships, also, may be very specialised, and in any of these the conservation of mutualisms is a key feature in conservation of the taxa involved. One well known example, a classic obligate mutualism, is the interdependence of yucca plants and yucca moths (*Tegeticula* spp., belonging to the small archaic family Prodoxidae). The moths are the only pollinators of the yuccas, whilst the developing seeds are the sole food of the developing caterpillars; even here, however, recent taxonomic studies have revealed a far greater richness of the moth species than earlier supposed (Pellmyr & Huth 1994).

Very broadly, the three traditional 'functional groups' of herbivorous Lepidoptera adopted widely by ecologists have been based largely on caterpillar feeding habits, as (1) specialists, using plants of a single species or genus; (2) oligophages, using multiple plant species within a single family or other restricted lineage; and (3) generalists, with more cosmopolitan feeding habits. More comprehensively, in contrast, Summerville et al. (2004, also Summerville & Crist 2002) classified forest moths into life forms of the host resource as a guide to interpreting changes in moth assemblage composition. He nominated five such guilds as (1) woody plant feeders; (2) herbaceous feeders; (3) dead or decaying vegetation feeders; (4) encrusting flora feeders; and (5) generalised feeders that transcend two or more of the above categories. As an example of this application, loss of trees in forests of Ohio was associated with lowered numbers of group 1 taxa, but overall richness was compensated by gains of additional herbaceous plant feeders. Knowledge of feeding guilds is clearly advantageous in interpreting changes in diversity, and in part helps to explain unexpectedly high levels of moth richness in some disturbed forest habitats. This theme is revisited in Chapter 7. The pattern detected by Summerville and Crist also reflected species turnover along a gradient of increasing habitat loss, in which different guilds replaced one another, with herbivory shifting from the canopy to the understorey layer, particularly in smaller plots.

The widespread habit of herbivory is also the major feature establishing some Lepidoptera as 'pests' through their depredations on crops, ornamental plants, stored plant products and other organic derivatives, with many species causing

widespread and severe economic losses. The converse situation also occurs – that some plant-specific Lepidoptera are valued as feeding on pest plants (weeds) and can be potent biological control agents in pest management. Most species involved as pests are moths, as a further factor influencing their public image, whilst very few butterflies (such as the cabbage whites, Pieridae, on brassica crops) are regarded as damaging pests. However, and in close parallel to Orthoptera (as noted by Samways and Lockwood 1998), serious pest species of moths or butterflies may have very close relatives that are respectively innocuous to human interests and severely threatened, in need of conservation attention. Some such closely related and generally similar-looking taxa may be very difficult to differentiate.

Unusually amongst larger groups of holometabolous insects, for which species-level identification relies very largely on the adult insects alone, the early stages of many Lepidoptera can also be recognised reliably to species level, particularly amongst the northern temperate region fauna. Substantial biological information accrues from studies of both caterpillars and adults, as the two active life history stages with very different biologies, and the resource needs of both are central to conservation management. Well illustrated synopses enabling identification of European butterflies and larger moths flow from the mid nineteenth century, largely the outcomes of hobbyist zeal, and have been followed by comprehensive guides for recognition of many caterpillars, in particular for those of other parts of Europe and North America – with outlines or some descriptions available for many other parts of the world or for particular taxa. The early impetus for this development was also from hobbyists, many of whom rear field-collected or captive-bred caterpillars to obtain cabinet-quality adult specimens, and gain considerable expertise in the discovery, identification and husbandry of immature stages. In parallel, information on seasonal developmental patterns, food plants and habits of many species has also accrued. Less definitive information, reflecting their lower general profile, is available for many Microlepidoptera (Chapter 2, p. 16), but compendia of biological information (such as that by Ford 1949, for Britain) and recognition guides based on indirect features (such as the form of leaf mines for some endophytic groups) still provide much stronger and more reliable specific information than on any other large insect group. Considerations of species' ecology and of assemblage richness and community interactions can commonly incorporate both caterpillars and adults, with either stage potentially available for evaluation as an intergenerational marker of change (Chapter 13, p. 242). However, as for adults, geographical bias in knowledge of immature stages is strong, and details of most tropical Lepidoptera, in particular, remain undocumented. The large-scale attempt to inventory the Lepidoptera of the Guanacaste World Heritage Site of Costa Rica (Miller et al. 2006) was based on light trap catches of adults and direct searches for caterpillars, and extended over almost 30 years from 1978. Every caterpillar found was isolated and documented individually, and reared to determine its fate in yielding either an adult or a parasitoid. Miller et al. estimated that about 9500 species of larger free-living Lepidoptera occurred at Guanacaste, and this total excluded a possible several thousand leaf-mining species. This long-term and thorough investigation remains unique for tropical biomes.

## Sources of information

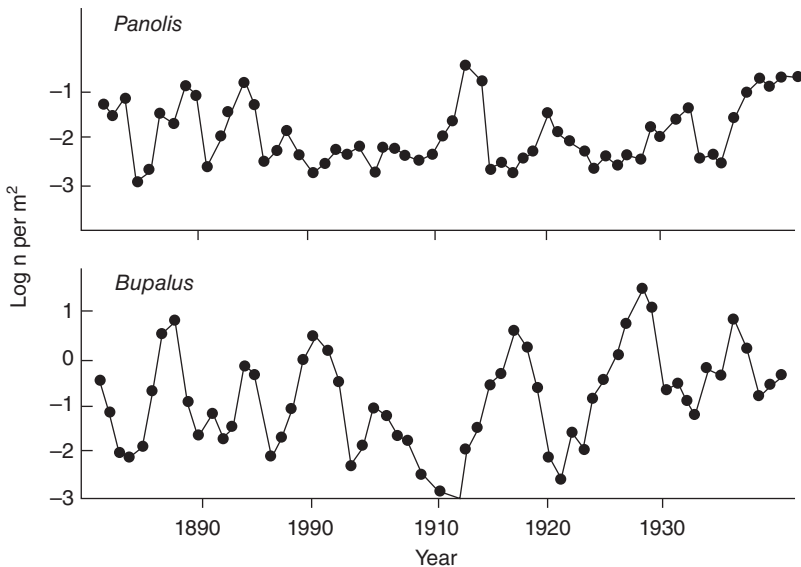
Publications on Lepidoptera biology and identification are thus far more extensive and varied than for most other insects (rivalled only by those on Coleoptera), and also more fragmented into different ‘interest groups’. Continuing documentation on Lepidoptera thereby has several distinct foci, in addition to that dealing directly with conservation matters.

- 1 Natural history observations, from hobbyists and others, stemming from records of incidence in time and space, as well as focus on life history details and ecology, with notes in a variety of outlets extending to compilation of handbooks and identification manuals for adults and larvae accessible to non-specialists. Much fundamental information has accrued, for example, from hobbyists in Britain through a variety of journals (some extending for more than a century of publication) and newsletters, nowadays in electronic or print formats.
- 2 More detailed ecological or ‘scientific’ contributions on systematics, biology and behaviour, often with quantitative/semiquantitative treatment of testable hypotheses. Studies range from those on single species or assemblages primarily addressing the insects themselves, to those employing Lepidoptera as ‘tools’ to help interpret ecological topics and questions. Relevant scientific contributions also encompass those dealing with studies of Lepidoptera in evolutionary biology and biogeography studies, in helping to illuminate much of the historical record that has determined the incidence and distribution of the recent fauna.
- 3 ‘Applied entomology’ contributions, extending from the above to aid understanding of the population dynamics, feeding ecology and specificity, dispersal and phenology of individual pest or beneficial species. The aim is to provide information that can be used to predict the species’ performance and impacts, and which can be used to suppress or enhance those impacts through practical management in relation to human needs.
- 4 Use of Lepidoptera more widely as models or surrogates, as signals of environmental wellbeing or change, through comparative studies of diversity or of presence and abundance of particular species across different sites or times and as potential tools to predict impacts of future changes (such as climate change). Any such study may apply to single species, assemblages or communities, particular natural or anthropogenic habitats or wider landscapes, and so focus on any of a wide range of scales.

Practising insect conservationists can gain much from the massive ‘applied literature’ in ecology, simply because details of knowledge on many key pest or beneficial taxa, including Lepidoptera, can be supported by economically justified funding and the need for that detail to refine management. Such detail is much harder to pursue for many taxa that are innocuous, and difficulty is enhanced for many species of conservation concern because their scarcity renders them intrinsically difficult to study or survey. Thus, much of the basic understanding of insect population dynamics (Chapter 6), has arisen from interpreting

long-term painstaking standardised counts of life stages of key pests in forests, orchards or field crops over many consecutive generations.

As one early classic example, comparison of the life systems of codling moth (*Cydia pomonella*) in Canada and Australia (summarised by Clark et al. 1967) showed how local environmental conditions may influence a key pest species. As another case, the introduced European cabbage white butterfly (*Pieris rapae*) has been studied in Australia far more intensively than almost any native Australian butterfly (Jones 1981, Waterhouse & Sands 2001), and its biology can be compared constructively with that in its native Britain (Richards 1940). Management for pests (aiming to reduce numbers) and for conservation (aiming to sustain or increase numbers) draws on the same kinds of ecological information, and the perspectives revealed by intensive studies on pests can at times complement the (usually far less) information available on rare species targeted for conservation. Contexts such as clarifying the roles of natural enemies, food quality and local environmental conditions, and their influences on abundance and fitness are important aspects of threat evaluation in conservation, and of understanding pest dynamics. A universal problem is how to interpret observed changes in numbers, and whether abundance varies naturally and significantly across generations – or, conversely, whether any marked change may be a real trend, either upward or downward, and lead to relief or concern (Chapter 6). The forms of numerical changes in pest moths (exemplified by classic studies on several univoltine pine-defoliating species in Europe, for which numbers in samples were plotted over 60 years, 1880–1940: Fig. 1.2) revealed substantial



**Fig. 1.2** Long-term population fluctuations interpreted from annual census counts of pupae of two univoltine pine forest moths in Germany over 60 years. The two representative species shown are (a) *Panolis flammea* (Noctuidae, the Pine beauty) and (b) *Bupalus piniarius* (Geometridae, the Bordered white) (Source: Varley et al. 1973. Reproduced with permission of John Wiley & Sons.).

natural variations and implied cyclic fluctuations over numbers of generations. Each species occasionally increased to serious defoliation-causing levels but at other times was relatively scarce (discussed by Varley et al. 1973). From a conservationist's viewpoint, normally supported by – at most – a few generations of information, such long-term variations are simply not apparent, and whether the limited data available are from an upward or downward part of the natural cycle may imply very different conservation need.

In general, information on 'how Lepidoptera work' based on such studies of common or easily available species and from hobbyist interests in many more obscure taxa, has provided most of the background available to guide studies for conservation, through demonstrating both general principles and the detailed idiosyncrasies of individual taxa. By their very elusiveness, many of the taxa of greatest conservation concern are difficult to study – and this is by no means restricted to those small of stature. Although the smallest member of its genus, the endemic Australian Ward's atlas moth (*Attacus wardi*, Saturniidae) is one of the country's largest moths, and was not seen for some 60 years after its initial discovery in Darwin (Northern Territory) (Braby & Nielsen 2011). Now known from six localities, it seems to occur very patchily over a small part of north-western Australia. Only very recently has its larval foodplant been determined (as *Croton habrophyllus*, Euphorbiaceae), and this grows along edges of monsoon forests, so giving clues on the critical habitat needed by *A. wardi*.

There remains the literature on Lepidoptera that deals more specifically with conservation, or primarily addresses practical or theoretical themes of conservation interest in the direct context of conservation. As noted in the Preface, books on Lepidoptera abound and well illustrated field guides and related handbooks are a major facilitator of interest in the group. However, until the last decade or so, the term 'conservation' occurred rather rarely in these, or was mentioned only as a brief afterthought. There are notable exceptions, mostly from Britain, western Europe or North America, where the urgency of conservation need was well appreciated and the possible consequences recognised and taken seriously. Thus, the two highly readable volumes on natural history of moths (Young 1997, Majerus 2002) both contain considerable information on moth conservation both as themes running through their text and as more emphatic specific chapters. More awareness, as expected, has been disseminated for butterflies, in many parts of the world, and includes attention to production of directories or lists of threatened taxa (Chapter 11). Many of these, and many research papers and reports, are cited in context here, but it is important to note also the deep roots of Lepidoptera conservation interest in the fates of individual species or, in some cases, local subspecies and, thus, in regional endeavours. Autecological studies on some such taxa have sometimes led to far-reaching appreciations of biological subtlety and of the importance of differences between closely related or co-habiting taxa. The considerable array of peer-reviewed documents is augmented by many consultancy and government agency reports of more limited circulation and which are amongst the 'grey literature' of conservation; these include much valuable information and, in some cases, are the only sources of data on the taxa they treat.

Likewise, the 'snippets' provided in short observational notes from hobbyists and others often include critical and important insights into incidence, behaviour

and biology of individual rare species; although it has been fashionable to denigrate ‘natural history’ in favour of more technical disciplines, good basic observational knowledge and understanding underpins many successful conservation efforts for Lepidoptera. As Young (1997) noted, amateur enthusiasts are ‘a mine of information’ on the biology of moths, ‘often including knowledge that is laboriously “rediscovered” by scientists later’. A major and vital facet of Lepidoptera conservation, setting it apart from much other invertebrate conservation, is the continuing strong cooperation and symbiosis between non-professional interests and scientists. The theme is central to Lepidoptera conservation and recurs in many contexts throughout this book. The continuing study of Lepidoptera and their wellbeing depends to a very large extent on the involvement and commitment of the wide range of people to whom these insects are in some way attractive and important.

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