

Habitat considerations for parasitic wasps (Hymenoptera)

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Abstract

Parasitic wasps operate at a high trophic level and, because of their biology, tend to be highly specialised, sometimes having very narrow host ranges with at least local monophagy a frequent outcome. These features, in addition to our poor state of autecological knowledge, render them particularly vulnerable in conservation terms and suggest that their habitat needs should be analysed differently from those of most other insects. The basic life history of parasitic wasps and some of the ways in which they interact with host populations and in communities are outlined. Then, against a background of very limited autecological data, and therefore somewhat speculatively, habitat parameters that seem likely to be of importance to parasitoids are discussed, largely by reference to the host relations and ecology of ichneumonoid parasitoids of Lepidoptera in N. W. Europe. Some considerations of environmental change are included.

Introduction

Despite difficulties in precisely defining ‘Habitat’ (Elton 1966; Dennis et al. 2003) and picking it out from a continuum involving also niche and biotope, considering the performance and interactions of organisms from that stance is fundamentally important (Southwood 1977). In a journal issue covering concepts of habitat in relation to insect conservation, it is appropriate to try to include the trophic level represented by parasitoids and, in particular, to explore whether the parasitoid life-history strategy raises special demands, different from those of other insects.

Although not all insect parasitoids are parasitic wasps (Eggleton and Belshaw 1992, 1993) and, indeed, not all organisms having an essentially identical functional biology are even insects (Eggleton and Gaston 1990), parasitic wasps are an overwhelmingly large group, comprising about a quarter of the entire British insect fauna, and this

account will be largely focused on them. I regret that it will also be strongly biased towards ichneumonoid parasitoids of Lepidoptera in N. W. Europe.

LaSalle and Gauld (1993) give a comprehensive account of the huge importance, and also vulnerability, of Hymenoptera in terrestrial ecosystems. The main characteristics of parasitic wasps that might suggest a different approach to considering their nature conservation needs in habitat terms from that of other insects are:

- (1) They operate at a high trophic level;
- (2) They tend to be abnormally specialised; and
- (3) Almost all species are very poorly known in autecological terms.

All three of these characteristics are likely to make them especially vulnerable to extinction (Shaw and Hochberg 2001); the first two for real ecological reasons, and the third on the optimistic

presumption that a focus on knowledge-based nature conservation effort is on the whole effective, but with the pessimistic rider that not enough is known about parasitic wasps to be able to engage them at all easily.

Basic life history

Rather more comprehensive descriptions of the basic life history of parasitic wasps can be sought elsewhere (e.g., Gauld and Bolton 1988; Godfray 1994; Gauld and Hanson 1995; Shaw 1997), but in essence they are free living as adults, and develop as grub-like larvae on or in the single body of another insect (which is usually immature) or, in a few cases, an arachnid. Insect and spider eggs are also used, either singly or such that an egg-sac's content serves as the single host unit. Development may be gregarious with respect to the host or solitary, and larvae may be internal or external to the host as they develop (respectively, as endoparasitoids or ectoparasitoids). The host is always killed as a result of the association, but there is an important dichotomy in the way this occurs: species that kill or irreparably immobilise the host at the time of attack are called idiobionts, while those whose hosts continue to function (usually continuing to feed, and being capable of self-preserving behaviours) for a time after being parasitised are termed koinobionts (Haeselbarth 1979; Askew and Shaw 1986). Not surprisingly, because almost all terrestrial insects are prone to attack, the early stages of parasitic wasps are themselves parasitized by both idiobionts that attack them after the original host has been consumed (pseudohyperparasitoids – typically attacking the cocoons of primary parasitoids) and by koinobionts that attack a primary koinobiont parasitoid while it is still developing in or on the host (true hyperparasitoids). True hyperparasitoids are usually obligatorily so, but pseudohyperparasitoids can often function facultatively as either primary or secondary parasitoids.

As a group parasitic wasps are both behaviourally (Godfray 1994) and physiologically (Quicke 1997) complex organisms, exhibiting much biological diversity. Variation in general life history is an important aspect of the evolutionary ecology of parasitic wasps as a group, and an appreciation of their varied characteristics is fundamental to try-

ing to understand their habitat requirements and their possible responses to environmental change. There is a well-supported tendency for the host ranges of idiobionts to be potentially wide (though in practice resource security may allow them to evolve as specialists) while that of koinobionts is more absolutely constrained by the physiological needs to adapt to a living host (e.g., Askew and Shaw 1986; Sheehan and Hawkins 1991; Althoff 2003). Many authors have adopted the ideas embodied in the idiobiont/koinobiont dichotomy but then slipped into regarding it as equivalent to ectoparasitism/endoparasitism, which is incorrect. While most (although not all) idiobionts are indeed ectoparasitoids, a substantial number of ectoparasitoids are koinobionts and have the same kind of host range parameters as the more familiar and numerous endoparasitic koinobionts. Although fewer in number, endoparasitic idiobionts tend to share the host range characteristics of ectoparasitic idiobionts.

Population dynamics and community structure

Insects and their parasitoids are extremely important components of terrestrial ecosystems, but it is also partly because of the substantial levels of specialisation, or at least community fidelity, exhibited by parasitic wasps that theoretical ecologists have taken them so strongly to heart. Indeed, the extent to which phytophagous insect populations and communities are regulated and structured 'top down' through host/parasitoid interactions (in contrast with 'bottom up' processes, or 'donor control': cf. Hawkins 1992, 1994) has engaged ecologists strongly over the past half century. Theory has generally run well ahead of empirical evidence (for readable accounts of some issues see Hassell 1986; Lawton 1986), but over the past few years some intensive field studies have provided robust tests and in many cases strong support for theoretical ideas. On the face of it, the enduring successes of various classical biological control programmes around the world might be taken as clear evidence that parasitoids can regulate host populations, but the possibility has been recognised (e.g., Hanski 1987) that the introduced parasitoid(s) may have merely caused a reduction in the host population to a point at which some other regulatory process can operate. Relatively recently,

however, analysis of long time-series data has shown not only that density dependence *per se* is a real phenomenon in insect populations (e.g., Woiwod and Hanski 1992), but also that regulation of insect populations by parasitoids can occur (e.g., Hassell et al. 1989; Bonsall et al. 2004; Redfern and Hunter 2005; and references therein). Similar analyses of long time-series data on host/parasitoid systems have confirmed that heterogeneity within populations (such that not all individuals are equally susceptible, cf. Hassell 2000) can underlie empirical cases of coexistence that contradict simplistic ecological models (e.g., Bonsall et al. 2002, 2004; and references therein), and in scaled-up habitat and landscape terms this is manifest in the great success and importance of the ideas of metapopulation ecology (Hanski 1999) in insect conservation. Additionally, within communities involving parasitoids, experimental manipulations, especially following the construction of quantitative food-webs, have started to unravel the extent to which apparent competition (cf. Holt and Lawton 1993, 1994) provides structure at various trophic levels (van Nouhuys and Hanski 2000; Morris et al. 2001, 2004; and references therein).

Some of the very extensive literature on population dynamics and community structure involving parasitoids will be traceable from the references given above, but further discussion of this vital backdrop is beyond the scope of this account – except to say that, although many of these considerations have been focused on the effect of parasitoids on hosts (as is the usual lot for parasites *sensu lato* – cf. Windsor 1995), there are obviously reciprocal effects on the parasitoids such that these and other aspects of community ecology will impact on concepts of ‘habitat’ for parasitic wasps in important ways. For example, different numbers of species of potential hosts and potential competitors, different levels of intensity or exclusivity of interactions, and both dynamic and stochastic issues surrounding the evenness of host occurrence in space and time, are aspects of ‘habitat’ that will all contribute to the short, medium and long term viability of particular parasitoid populations.

Autecology

It is, however, our poor knowledge of the autecology of individual species of parasitic wasps that dictates how much – or how little – practical

understanding can be brought to a discussion of their habitat needs. As Greene (2005) has stressed in more general terms, real ecological understanding can only follow from a much deeper knowledge of the actual organisms than we possess, and much more effort needs to be directed towards basic natural history studies. This is overwhelmingly true of parasitoids.

To understand what is meant by poor autecological knowledge, consider how we might address the exact habitat needs of (say) a butterfly species. We would scarcely be willing to start without knowing at the very least something about its gross distribution, spatial and temporal variation in its abundance, the kind of terrain in which it occurs, its food and its life cycle details (knowing about its parasitoids and other natural enemies is also important, but sadly these aspects are often omitted altogether). For most species of parasitic wasp we do not know *any* of that with certainty – and the few data we do have are not definitive, in the sense that a couple of capture records does not constitute a distribution (either in space or in time), and a rearing record does not provide a host range. On the whole we know in rough terms what most *groups* (genus, tribe or subfamily) of parasitic wasps do, but we have reliable host data for probably less than a quarter of *species* (even in Britain) and anything approaching rounded autecological knowledge of probably a lot less than one in twenty. As for distribution, our perceived knowledge is little more than a matter of which of the very few hymenopterists interested in parasitoids has lived (or collected) where.

Even when a host of a parasitoid is reliably known, it still needs to be assessed in relation to the host range (both potential, and realised at a particular location) of the parasitoid species (Shaw 1994). It is important, too, to understand that congeners (i.e. very closely related species) often have widely different breadths to their host range, whether they are koinobionts (e.g., Shaw and Horstmann 1997) or idiobionts (e.g., Schwarz and Shaw 1999). The problems involved in assessing host range, and suggestions for overcoming them, have been discussed elsewhere (Shaw 1994); here it seems most appropriate just to mention the paradox that the more ‘important’ an insect appears to be to humans (e.g., as a crop pest, or as a parasitoid of that pest) the more confused appears to be the published information about which species

function as parasitoids of it, and/or the host ranges of the parasitoids that really do attack it (e.g., Shaw 1981; Noyes 1994). There is still an unfortunate dependence by some ecologists on works such as W. R. Thompson's (1944–1958) massive literature abstract 'Catalogue of the parasites and predators of insect pests' for their data; and, equally unfortunately, taxonomic revisions and key works for parasitoids are often still constructed with insufficient suspicion of old host records, which consequently tend to be simply repeated without comment, thereby giving the quite probably erroneous record an apparently modern confirmation.

Habitat needs

Leaving aside the poor state of our knowledge, we can still try to ask what habitat features a species of parasitoid needs in order to maintain a persistent population at a 'site'. There are some extremely obvious requirements:

A host population

This has to have some stability, whether in static or metapopulation terms – if the latter, the dispersal characteristics of the parasitoid have to be sufficient to deal with the transience of patch occupancy by the host. The rather slight existing evidence on the dispersal abilities of parasitic wasps is equivocal: while Horstmann (1988) found a much higher species diversity of adult ichneumonids sampled on small North Sea islands off the German coast than could be explained by host presence, others have advanced evidence of low colonisation rates of parasitoids in new host populations and concluded that habitat fragmentation has a worse effect on parasitoids than on their hosts (Kruess and Tscharrntke 1994; van Nouhuys and Hanski 1999). No doubt in practice there will be a huge range of variation in this, rendering generalisation meaningless, but dispersal will obviously only be successful if potential foundresses find suitable conditions on arrival, bringing us back to the generally high level of habitat demand (i.e. including host presence) that appears to characterise many parasitic wasps. Because of the haplo-diploid mechanism of sex determination that is general to

Hymenoptera, there is a more insidious, genetic problem that may effect populations of parasitic wasps resulting from a single foundress: if sex determination in that species is at a single locus (which is frequent, though not universal) there is, in the absence of genetic reinforcement, a likelihood of an increasingly high proportion of the population becoming functionless as diploid males (Cook and Crozier 1995).

Interestingly, even specialist parasitoids of a particular host can differ substantially in their dispersal characteristics, as is shown by two koinobiont larval parasitoids of the nymphalid butterfly *Melitaea cinxia* (Linnaeus) (van Nouhuys and Hanski 2002; Kankare et al. 2005). This immediately raises issues of spatial scale and its interplay with stochasticity and, partly because of differences in other biological characteristics of the two parasitoids, they have different roles and propensities to cause patch extinction in the host metapopulation in S. Finland as well as different potentials for their discovery of, and survival in, patches freshly occupied by the host (Lei and Hanski 1997, 1998; van Nouhuys and Hanski 1999). Obviously, if a monophagous parasitoid drives its host extinct locally, it too will disappear: while this does not normally happen in an irreversibly permanent way in functional metapopulations as a whole, the risk to both host and parasitoid is intensified if habitat patches become isolated and the metapopulation structure starts to break down. It is important to realise that the possible role of parasitoids in irreversible local extinctions of insects that have suffered a loss of metapopulation structure has scarcely ever been seriously investigated by conservationists. However, the threats posed by habitat fragmentation are in fact much more likely to impact on specialised parasitoids than their hosts (e.g., van Nouhuys and Hanski 1999), not least for the obvious reason that the parasitoids will necessarily be existing at lower mean incidence levels and therefore be more likely to be eliminated by stochastic events, as well as being highly vulnerable to periods of host scarcity (Kruess and Tscharrntke 1994).

The demonstration in the *M. cinxia* metapopulation in S. Finland that parasitoids can cause patch extinction of the host, and the strong circumstantial evidence that in Britain the regular pattern of local extinctions seen in the lycaenid butterfly *Celastrina argiolus* (Linnaeus) are driven

by its specialist ichneumonid parasitoid *Listrodromus nychthemerus* (Gravenhorst) (Revels 1994; Asher et al. 2001), suggest that the prospects for persistence of specialist host–parasitoid relationships will be greatly enhanced by metapopulation structure, or at least the presence of refugia for the host. Nevertheless, what seem to be discrete and isolated populations of insects often appear to co-exist locally with their specialist parasitoid(s) over long periods. Although unfortunately empirical data are practically non-existent, there are perhaps two extreme ways of interpreting this (though with the proviso that more complicated ecological factors may be overwhelmingly more important). One is to dismiss it as fortuitous, if it is supposed that the presence of the parasitoid will pose a continuous threat to the host, always increasing its prospect of local extinction. However, although supporting formal evidence is on the whole lacking, there is also the other possibility that the presence of parasitoids might sometimes stabilise the host population, in the sense of tending to prevent it from exceeding the site’s carrying capacity and/or reaching the trigger for catastrophic density dependant mortality such as disease or mass starvation. Therefore it might be argued that specialist parasitoids of threatened hosts should be conserved not only for their own sake, but also for that of the host. Which tendency predominates might be expected to depend strongly on the life-history features of the host: a series of detailed case studies on genuinely isolated populations of different host species and their specialist parasitoids that appear to be persistent for lengthy periods might help to elucidate this. But however a particular host–parasitoid relationship is functioning, the best general conservation strategy will undoubtedly be to ensure that metapopulation structures can persist such that the host–parasitoid interaction itself is not threatened overall.

Other aspects of the ‘host population’ are complicated by what is meant by the ‘host’. Some parasitoids are absolutely monophagous, in which case the concept of ‘host’ is clear enough, and others have narrow host ranges which can (and do) result in many persistent populations being locally monophagous. This can operate at a very local scale – for example there are likely to be many populations of the butterfly *Polyommatus icarus* (Rottemburg) in Britain that are potentially capable of supporting populations of one or more

of the several oligophagous parasitoids that are entirely restricted to polyommataine Lycaenidae without the presence of other potential hosts – or it can be seen operating over very large areas; for example, the parasitoids that are specialists of say *Gonepteryx*, or *Limenitis*, or *Lycaena* (s.l.) species of butterflies find only one host in Britain but two or more in Europe as a whole. For local monophagy to be viable, the life cycles of the host and parasitoid have to match, but there are a number of parasitoids that are plurivoltine but use only univoltine hosts. These range from rather generalist species (often idiobionts) – which are perhaps likely to make relatively low demands on the availability of any particular host species – to highly specialised species with an absolute requirement for different sets of hosts to be present at the appropriate times of year for completion of the annual life cycle. Parasitoids with these demands are typically koinobiont endoparasitoids, and usually they overwinter as larvae inside diapausing larval hosts. Some examples in the rogadine braconid genus *Aleiodes* are given by Shaw (2002), and it is clear that many cases exist in large sub-families such as Microgastrinae (Braconidae) and Campopleginae (Ichneumonidae) (M. R. Shaw unpublished data), but the reality is that we know far too little about the host ranges of parasitoids, at the species level, for these needs to be easily detected and understood.

A couple of interesting habitat-related situations associated with changes in the host spectrum available to a particular parasitoid are worth noting as opportunities for further study. The first concerns the microgastrine braconid *Pholetesor circumscriptus* (Nees), which is a plurivoltine parasitoid of several gracillariid leaf-miners especially in the genera *Phyllonorycter* and *Parornix* (also sparingly using certain grass-mining Elachistidae over the winter). It is especially abundant as a parasitoid of the very few *Phyllonorycter* species that mine through the winter, on which completion of its annual life-cycle disproportionately depends. The arrival and explosive spread in Britain of *Phyllonorycter leucographella* (Zeller), which mines through the winter on *Pyracantha*, often at high density, has (at least in built-up areas where the non-native foodplant is often planted) given the parasitoid an enormous population boost, as it has adopted *P. leucographella* to its host range very success-

fully and typically achieves a very high level of parasitism on it (Godfray et al. 1995). Whether or not this dramatic improvement in the habitat for *P. circumscriptus* is significantly influencing its local representation in the parasitoid complexes of its other gracillariid hosts remains to be investigated. The second concerns the rogadine braconid *Aleiodes coxalis* (Spinola), which is a partly plurivoltine parasitoid of various Satyridae, that can fit in an extra brood on *Thymelicus lineola* (Ochsenheimer) (but not other Hesperidae) where that host occurs. In this way it can attain high populations where *T. lineola* is abundant but, again, it has not been ascertained whether or not the relatively recent spread of *T. lineola* in S. E. England (Asher et al. 2001) has depressed co-occurring populations of satyrids through apparent competition mediated by *A. coxalis*.

Insect conservationists contemplating introductions or reintroductions should always assess the risk that a newly introduced potential host might boost the abundance of a shared parasitoid to the extent that it then becomes a bigger threat to its pre-existing host.

Host foodplants (tritrophic effects)

There is a great deal of literature on tritrophic effects involving phytophagous hosts and their parasitoids (e.g., Le Corff et al. 2000; Lill et al. 2002; Ode et al. 2004; and references therein). Much of the early work is included in a series of extensive reviews by Vinson (1976, 1981, 1984) that survey the various ways in which parasitoids find acceptable hosts, revealing several mechanisms whereby parasitoids may be less able to use a given oligophagous host on a part of its food-plant range. In some cases this arises through secondary plant metabolites rendering the host more or less toxic to its parasitoids, but relatively recently it has also become clear that some plants are able to respond to feeding damage caused by insects by emitting chemical signals that attract parasitoids (Tumlinson et al. 1993; Moraes et al. 1998; Vinson 1999). The plant composition of habitats supporting oligophagous hosts and their specialised parasitoids, or less specialised parasitoids able to use a broader range of hosts, might therefore be expected to influence the suitability of the habitat for particular parasitoids very pro-

foundly, perhaps even leading to the competitive exclusion of some if parts of the host populations were able to exist in partial or complete refugia from some of the parasitoids.

Askew and Shaw (1986) give an example of two koinobiont parasitoids that overwinter inside the young larvae of their lymantriid moth host, *Leucoma salicis* (Linnaeus), and have opposite effects on the timing of the latter breaking its winter diapause. Because the two principle plants used at the study site differ appreciably in their time of bud burst, one plant is rendered apparently completely unsuitable for one of the parasitoids purely on temporal grounds, but possibly even more suitable to hosts supporting the other than it is to unparasitised hosts. It was shown by van Nouhuys and Hanski (1999) that differing levels of parasitism of the butterfly *Melitaea cinxia* in S. Finland on each of its two foodplants had profound ecological consequences, though in this case the reason for the difference was less clear. A recent study on parasitoids associated with saproxylic beetle hosts in boreal spruce-dominated forests in Sweden has indicated that only a management strategy promoting the widest diversity of dead wood types would preserve the entire ichneumonoid assemblage, and that the sensitivity of parasitoids to habitat change is greater than that of their hosts (Hilszczański et al. 2005).

Food for the adult

Parasitic wasps are either broadly (cf. Ellers and Jervis 2004) pro-ovigenic (the newly emerged female has virtually her full complement of eggs ready for oviposition) or synovigenic (the female matures her eggs successively during her adult life). In the former case the eggs usually have little or no yolk, and are placed inside a living host from whose haemolymph nutrients are absorbed by the egg. Pro-ovigenic species are usually (perhaps invariably) koinobionts and often have relatively short but very active lives, and sources of sugar (nectar, honeydew) are extremely important to them, while protein intake is not usually needed. Synovigenic species, on the other hand, are usually longer-lived and require also proteins in order to yolk their typically much larger eggs, which do not normally take in nutrients once laid. Pollen might sometimes be

important, but often they get these by feeding on haemolymph from their hosts (either ovipositing in/on the same or different individuals – cf. Jervis and Kidd 1986). In some cases they actively seek a range of other insects on which to feed (e.g., Zijp and Blommers 2002). Because of a general need, habitats in which sources of sugar are abundant are particularly likely to be good for parasitic wasps, as parasitic hymenopterists who site traps between host-rich and flower-rich sites are well aware. Despite the importance of flowers (Jervis et al. 1993), however, less evident sources of sugar such as honeydew may be even more significant in many habitats.

Adult diapause and roosting sites, and shelter

Adult females of quite a lot of taxa of parasitic wasps either aestivate or hibernate, or do both (especially in the case of a few spring-active univoltine species). Favoured sites include grass tussocks, behind loose bark, or dense (evergreen) aerial vegetation (e.g., *Juniperus*, *Taxus*), or the man-made habitat, thatch. Different species show strong preferences for given sites. However, a very large number of parasitic wasps pass the winter in other ways – as larvae inside hosts, or as pupae or prepupae.

Activity in feeding and host-searching is interrupted both by diurnal cycling (e.g., nightfall) and by inclement weather. The importance of roosting sites in a habitat can be dramatically revealed by beating dense shrubs such as *Juniperus* in wet weather or at dawn, or by sweeping tall sparse grassland on dewless summer mornings before sunrise.

Studies by Juillet (1964) on flight (hence host-searching) behaviour of a range of Braconidae and Ichneumonidae showed rather varied responses to different weather conditions, but a uniform depression of activity with increasing wind speed above about 150 feet/min. As this is quite a low wind speed, sites lacking shelter may therefore be less supportive of parasitic wasps than otherwise equivalent sites that provide it. However, it is impossible to relate Juillet's (1964) study to the more inclusive insect data provided by Williams (1940) or, indeed, to discern possible differential susceptibilities of parasitic wasps in the latter study.

Mating sites

Although many insects have elaborate territorial courtship rituals that involve physical aspects of the habitat, parasitic Hymenoptera tend to be rather more basic in their activities such that females are usually mated very swiftly, more-or-less at their emergence sites (although courtship may still be behaviourally complex). Habitat features are therefore unlikely to play much of a part in courtship and mating for most parasitic wasps, though there are exceptions to this generalisation as a few taxa produce male swarms (Tobias 1998, 2002), and some of these centre the activity on a prominent tree or bush.

Refugia, and divisions of space

In addition to these very basic considerations, there are several other points of importance. The first is that parasitoids in general may not be able to exploit all situations in which potential hosts exist, and the concept of refugia can explain various observed patterns (cf. Hochberg and Hawkins 1992; Hawkins 1994). Examples of the life-histories that amount to refugia from parasitoids in a survey of parasitism of the order Diptera were given by Shaw and Askew (1978). Frequently a given host species is subject to differential attack by parasitoids over its distributional range. A simple example, involving only altitude, is given by Randall (1982); more complex examples involving tritrophic interactions have already been discussed.

Furthermore, while many parasitoids search only in the particular precise locations in which their particular narrow range of hosts occur, others have potentially very wide host ranges but still concentrate their search in only a sector of the overall habitat. A good example is provided by the two similarly sized, abundant and widespread British *Gelis* species, *G. areator* (Panzer) and *G. agilis* (Foerster), both of which have very wide host spectra involving the same sort of cocoons and cocoon-like structures (Schwarz and Shaw 1999), but *G. areator*, which is fully winged, searches largely on trees and bushes, while the apterous *G. agilis* is virtually confined to the field layer. Perhaps even more tellingly, given species of aphids alternating between trees and low plants at different times of year are generally attacked by

different parasitoids (Starý 1966). In fact a rather sharp division between low plants and trees/bushes as searching environments for parasitoids of herbivores seems to be very general and few use hosts from both, whatever the breadth of their host range. This trend is also clear in many Tachinidae (Diptera), parasitoids whose host ranges are in general taxonomically rather more diffuse than is usual for parasitic wasps (cf. Belshaw 1993).

There are, of course, whole suites of species of parasitic wasps characteristic of particular biotopes, which in some cases have as yet unexplained distinctive characters: for example, species of parasitic wasps associated with reed-beds and fenlands are usually significantly more marked with orange than their congeners. In some cases these fen specialists are dependent on host species only found in such places, but others appear to use hosts in the fenlands that are also found elsewhere.

Finally, it is perhaps worth stressing that the geographical range of a specialist parasitoid would not necessarily be expected to match that of its host any more than we would expect to find (say) all oak-feeding insects wherever there is a natural abundance of oak.

Climate change

Climate change consequent on global warming is likely to impact strongly on parasitoids because it will change the characteristics of their habitat. Apart from the high probability that substantial vegetational change will mask all other effects, however, there are relatively few situations in which obvious outcomes seem predictable. One fairly strong possibility is that hosts and their parasitoids will sometimes become asynchronous. This could occur in one of two ways. Either the major developmental cues of temperature and daylight might be balanced differently in host and parasitoid, in which case a gap in synchrony would be expected to arise as the thermal regime changed, or else the development rate at different temperatures will differ for host and parasitoid, again leading to asynchrony under novel temperature conditions. This might happen in quite subtle ways, as for example when mobile hosts are able to optimise their thermal experience in ways in which static parasitoid cocoons are not, and plurivoltine parasitoids that successively attack

different cohorts of the same generation of a univoltine host (e.g., *Cotesia* parasitoids of Melitaeini butterflies) may experience appreciable disruption. More generally, for specialists, when the host's life cycle gets ahead of the parasitoid's, species of the latter that have the narrowest window of opportunity for attacking their host will presumably suffer the worst, and if the parasitoid is the more advanced then the species that potentially have long adult lives will presumably fare best. Species with wide host ranges will obviously be more likely to retain synchrony with at least a part of their potential host range than absolute specialists. In all of these respects it looks as though in general some groups of idiobionts are likely to survive the disruptions of climate change better than most koinobionts, but this is crude speculation and individual species will no doubt respond in individual and perhaps surprising ways.

Agrochemical toxins

Apart from habitat fragmentation, one of the profound changes over the past half century in Britain has been the increase in insecticides applied in agriculture. As these have become increasingly sophisticated and insect-specific, fears about their direct effect on vertebrate life have been largely controllable, and very little research has been directed towards their effect on off-crop non-target insect populations, although the phenomenon of pest resurgence (Hardin et al. 1995) and economic concern for the effect of insecticides on within-crop natural enemies of the target species has resulted in a little research relevant to the crop environment (cf. Longley et al. 1997; Haskell and McEwen 1998; Desneux et al. 2004). However, both short-term and long-term studies seem to be lacking on the relative toxicity to different insect groups (and trophic levels) of low dosages of pesticides, i.e. at off-crop levels, having disruptive effects on insect development.

As a persistent collector of a wide range of the early stages of terrestrial insects and arachnids from which to rear parasitoids, I have a reasonably rich experience of 'good' and 'bad' sites, regarding 'good' ones as the places where common and widespread phytophagous insects have rare parasitoids (rare insects in the host groups tend also to be present, of course, but it is the parasitoid fauna

of the common and more widespread hosts that is most indicative). Trying to think of what fairly reliably constitutes this ‘goodness’ in a site of a particular biotope, I can think of three habitat factors: (i) reasonably large size, (ii) continuity, at whatever successional stage, and (iii) for parasitoids of folivores, its effective isolation from conventional arable or orchard agriculture. It seems to me that this last is a crucial factor in habitat quality that we may be overlooking, and it may help also to explain why brownfield sites (typically surrounded by buildings, not arable agriculture) and even suburban gardens rather paradoxically hold good populations of uncommon insects, sometimes including otherwise very elusive species of parasitoids (e.g., Owen et al. 1981). An ongoing study (J. Memmott, personal communication) comparing overall parasitoid food webs on organic and conventional farms may provide some measure of biodiversity loss at this trophic level associated with agrochemicals, but otherwise too little formal attention has been paid to the possibility that this is a major problem.

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