

Parasitoids

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Introduction

Parasitoids are insects whose larvae develop by feeding on the bodies of other arthropods, usually insects, but also spiders and centipedes. It has been estimated that parasitoids may make up 20–25% of all insects. In addition to their high diversity and prevalence, the study of parasitoids has been particularly important because they: (a) can be used as biocontrol agents to combat agricultural pests, and (b) have proved to be excellent systems for investigating outstanding questions in the study of behaviour, ecology and evolution. *See also: Parasitism*

Parasitoid Life Styles

There are likely to be one to two million parasitoid species (based upon an estimate of eight million insect species). These are predominantly in the Hymenoptera (the ants, bees, sawflies and wasps), but there are also species of parasitoids among the Diptera (true flies), Coleoptera (beetles), Lepidoptera (moths), Neuroptera (lacewings) and Trichoptera (caddisflies). To a large extent, the different parasitoid life styles are defined by the larval feeding habits, and this section briefly outlines the different possibilities, and the terminology that is used to describe them. Further details can be found in chapter one of Godfray (1994).

Attack

Parasitoids can be divided according to the number and type of species that they are able to parasitize. Some parasitoid species are generalists, being able to use several host species, while others are specialists, being able to develop on only one host species. Some parasitoids are parasitoids of other parasitoids, termed hyperparasitoids. Obligate hyperparasitoids can only develop as parasitoids of parasitoids, while facultative hyperparasitoids are also able to attack unparasitized hosts. Hyperparasitoids are often referred to as secondary parasitoids and cases have been recorded of tertiary parasitoids: parasitoids of parasitoids of parasitoids!

Female parasitoids lay their eggs either on or in the host or nearby. If the egg is laid nearby then parasitism ensues if the host eats the egg, or if larvae locate the host. In the case of hymenopteran parasitoids, females use highly specialized ovipositors to lay eggs, and in

some cases sting the host. In some species the sting kills the host, while in others there is only temporary paralysis, with the host recovering to continue feeding. The ovipositor can be several times the length of the body, which can allow the female to reach hosts that are well within substrates such as trees or fruit ([Figure 1](#)).

Figure 1



The hymenopteran parasitoid *Megastigmus stigmatizans* (Torymidae). Note the long ovipositor. Reproduced with permission from Stone G and Csóka G (eds) *Oak Gallwasps of the Western Palearctic*. London: Ray Society, Natural History Museum (in preparation).

Parasitoids of holometabolous insects such as butterflies, moths, beetles and flies can be divided upon the basis of the host stage that they attack. Different species can be egg parasitoids, larval parasitoids, pupal parasitoids or adult parasitoids. In some species the female lays eggs in one host stage, but the larvae do not kill the host until it has entered a later stage, and these are labelled following the two stages, such as egg–larval or larval–pupal parasitoids.

Growth

Parasitoids can be divided dependent upon where and how many develop within a host. Some species are endoparasitoids, developing within their hosts, while others are ectoparasitoids, who live externally and feed with mouthparts that are buried into the host. In solitary species only a single parasitoid is able to develop within a host, while in gregarious species several individuals (ranging from two to thousands, depending upon species) are able to develop on a single host. The larvae of solitary species are often equipped with fierce mandibles with which they kill other larvae developing in the host. The occurrence of such within-host competition can make it very hard to evolve from the solitary to the gregarious state ([Godfray, 1994](#)).

Parasitoid species that allow hosts to continue to grow after parasitism are called koinobionts, while species where the parasitoid larvae must make do with the host resources present at oviposition are termed idiobionts. Koinobionts either delay their development or feed only on host organs that are not vital. Parasitoids whose sting kills the host are all idiobionts.

Sex and reproduction

While some parasitoids are sexual, producing males and females, others reproduce asexually through parthenogenesis. In some cases parthenogenetic reproduction is forced upon the species by intracellular bacteria, while in others the cause is not known. Within the Hymenoptera, sex determination is haplodiploid, with diploid females developing from fertilized eggs, and haploid males developing from unfertilized eggs. One important consequence of this is that by altering the proportion of eggs that she has fertilized a female is able to control the sex ratio of her offspring. This relatively simple control has allowed natural selection to produce females which alter the sex of their offspring (termed sex allocation) in response to a number of factors, such as host size and the presence of other females (Godfray, 1994). This has led to studies upon parasitoids providing some of the best evidence for adaptive control of sex allocation, which in turn provides some of the best evidence for the adaptationist approach to evolution. *See also: Reproduction and life cycles in invertebrates*

Why are there so many parasitoids?

An obvious answer to this question is that there are so many host species to exploit. However, there are several reasons why speciation rates may be higher in hymenopteran parasitoids (Godfray, 1994). First, their haplodiploid genetics can lead to higher rates of molecular evolution: the rate at which favourable mutations are fixed is predicted to be higher in haploid species than in diploid species. Consequently, two populations might have to be geographically separated for a shorter time to speciate. Second, high rates of sibmating occur in many species and it has been suggested that this may increase the speciation rate because it can divide populations and increase the rate of random genetic drift. Third, the distribution of Wolbachia infections has been shown to differ in the hymenoptera from other insect groups (West *et al.*, 1998). Wolbachia are a group of intracellular bacteria that distort the reproductive tissues of insects in a number of ways. Importantly, one consequence of Wolbachia is reproductive incompatibility between individuals with different types (or absence) of Wolbachia. *See also: Speciation and Wolbachia*

What determines how many parasitoids attack a host species?

Much research has focused on this question because attempts to address it can be made with parasitoid lists that are already published (see Godfray, 1994; Hawkins, 1994). However, there are possible problems as the data collected from different sources can differ in a range of potentially important factors such as sample size, and geographic range or season sampled.

The clearest pattern to have emerged is the importance of feeding niche. Usually, six categories of host feeding niche are distinguished: (1) external folivores, (2) species that

feed in spun leaves, (3) leaf-mining insects that feed inside the leaf lamina, (4) gallforming insects, (5) species that feed inside stems, in wood, or within buds, fruits, flowers and seeds, and (6) root-feeding insects. These categories are ordered on the basis of concealment of the host within the host plant. [Hawkins \(1994\)](#) has shown, in both temperate and tropical data sets, that leaf-mining species possessed the highest number of parasitoid species attacking a host species, with a trend to lower numbers of species on both less and more concealed hosts.

At present, there are three possible explanations for this pattern ([Godfray, 1994](#); [Hawkins, 1994](#)). First, parasitoid diversity may be determined by the relative rates of recruitment and loss of parasitoids on different host species: (a) recruitment is greater on less concealed hosts, and (b) mortality due to factors such as predation is less on more concealed hosts, leading to less loss. These factors combine to create a peak at intermediate concealment. Second, parasitoid diversity may be determined by the size of the host population available for parasitoid attack. A lower proportion of individuals can be found of more concealed hosts ('refuges'), and so fewer parasitoid species can be maintained. As hosts become less concealed, more can be parasitized, and so the number of parasitoid species that can be maintained is increased. However, in the least concealed hosts, parasitoid populations are able to build up to sufficient numbers that they significantly depress the size of the host population, which can then maintain fewer parasitoid species. Third, the hosts feeding in some niches (e.g. leaf miners) are ecologically and taxonomically more uniform than those in others, and this leads to greater opportunities for the transferring or sharing of parasitoid species among hosts, which would lead to greater diversity per host.

[Quantitative parasitoid food webs](#)

Recently there has been a move to the construction of quantitative host–parasitoid food webs in order to address diversity and community level questions ([Memmott and Godfray, 1994](#)). A quantitative food web is one in which information is collected on the relative abundances of host plants, host insects and parasitoids. This distinguishes this type of webs from connectance webs, where only the presence or absence of an interaction between two species of host and parasitoid is recorded, and semiquantitative webs, where the relative abundances of different parasitoid species on their hosts are recorded.

Quantitative parasitoid food webs offer excellent opportunities for addressing a number of questions that cannot be addressed with other systems ([Memmott and Godfray, 1994](#)). These range across topics such as determining the causes of the number of parasitoids attacking hosts, determinants of parasitoid host range, potential for apparent competition, host–parasitoid dynamics, as well as offering potential for investigating the consequences of factors such as season and host abundance.

To date, the number of quantitative parasitoid webs published is small (although increasing), and so broad generalizations cannot be made. However, some points have already arisen

from a tropical leaf-miner–parasitoid web and a temperate aphid–parasitoid web. First, the number of parasitoid species reared from a host has been shown to be strongly influenced by sample size. Second, the number of parasitoid species attacking aphid species is significantly lower in species that are ant attended. Third, endoparasitic koinobionts have much narrower host ranges than ectoparasitic idiobionts, probably because their life style requires greater adaptation to the host.

Parasitoid diversity in the tropics

The diversity of most types of organisms increases towards the equator. However, parasitoid tropical diversity is either lower than or similar to that in temperate areas (Gauld and Gaston, 1994). While there are possible problems with the collection methods used (e.g. malaise traps and sweep netting), it seems clear that, at the very least, parasitoid diversity does not increase to the same extent that their host diversity does when going from temperate to tropical areas.

Three possible explanations for this pattern have been suggested. First, the resource fragmentation hypothesis suggests that the increased diversity of hosts in the tropics leads to the density of each host species dropping to the point where they cannot support specialists. Second, the predation hypothesis suggests that predation on hosts and parasitoids in the tropics is greater due to increased ant abundance and the year-round activity of predators and hyperparasitoids. Third, the nasty host hypothesis suggests that tropical woody plants have more chemical toxins than their temperate counterparts. Tropical herbivores therefore contain more toxins, and so parasitoids must be more specialized to deal with these. This could reduce parasitoid diversity because it: (a) limits the numbers of generalist parasitoids, and (b) reduces the probability of host transfer by specialists.

Host Defence and Parasitoid Counter-defence

Host insects will be selected to avoid parasitism by parasitoids, and parasitoids will be selected to overcome any defensive measures. There is therefore opportunity for reciprocal evolutionary change (coevolution) between hosts and their parasitoids. This coevolution could be diffuse, between a number of species, or tight, between a pair of interacting species. The factors that are involved in host defence and parasitoid counter-defence range from behavioural (e.g. hosts moving less to avoid detection by parasitoids that use vibrotaxis in host location) to physiological (e.g. hosts' immune response) (Godfray, 1994; Kraaijeveld *et al.*, 1998). This section will concentrate on the latter, because this is a rapidly advancing area and more is known. This work has concentrated on koinobiont endoparasitoids, because it is the still-living host that can mount an immune response. *See also: Coevolution: parasite–host*

Host defence

Possibly the primary host defence is encapsulation, the cellular immune response with which arthropods defend themselves against foreign bodies (Godfray, 1994). Certain cells in the haemocoel recognize foreign bodies such as a parasitoid egg or larvae and adhere. These then rupture and cause other cells to aggregate to the parasitoid, forming a capsule (encapsulation). In most species the capsule then melanizes and hardens, killing the parasitoid through asphyxiation or the release of toxic substances. It has been shown that genetic variation exists in the ability of hosts to encapsulate hosts (Kraaijeveld *et al.*, 1998). This variation occurs between species, between populations of the same species, and between individuals of a single population. It has been suggested that this variation reflects variation in circulating haemocyte concentrations. *See also: Immunology of invertebrates: cellular*

Why should such genetic variation exist? One explanation is that there is a cost to a higher encapsulation ability. Evidence for this comes from an experiment by Kraaijeveld and Godfray (see Kraaijeveld *et al.*, 1998) who artificially selected for encapsulation ability (resistance) in *Drosophila melanogaster* against the parasitoid *Asobara tabida*. Artificial selection increased the proportion of flies that could encapsulate parasitoid eggs from 5 to 60%. However, this increased encapsulation ability came at the cost of decreased competitive ability when food was limiting. A further experiment selecting for resistance in *D. melanogaster* against the parasitoid *Leptopilina boulardi* has shown similar results. In both cases, the reduced competitive ability appears to come at least partly from reduced rates of larval feeding, possibly because resources used for haemocyte development must be diverted from feeding. *See also: Drosophila as an experimental organism*

Parasitoid counter-defence

Parasitoids have evolved a variety of ways to counter host defences. In some species the parasitoid is able to reduce the immune response with venom or symbiotic viruses that are injected during oviposition. Particular attention has been focused upon the polydnaviruses (PDVs) that are injected by adult species of endoparasitic wasps belonging to the families Braconidae and Ichneumonidae (Beckage, 1998). These viruses kill and/or alter the behaviour of haemocytes, leading to less efficient adhering by haemocytes, and an encapsulation response that is less likely to be successful. Another demonstrated mechanism of action is the virus-like particles (VLP) with which *L. boulardi* and *Venturia canescens* coat their eggs, and which prevent haemocytes recognizing the eggs as foreign. These different mechanisms may interact. For example, it has been suggested that in braconid wasps, venom has a synergistic effect with PDVs, allowing the virus to act at much lower doses than it would normally.

Another way in which parasitoids can avoid encapsulation is by the site of development. Some species develop in tissues such as the brain where circulating haemocytes do not occur. One species, *Ascaris tabida*, has been shown to have 'sticky' eggs that adhere to

the fat body and other host tissues, which makes encapsulation more difficult. *A. tabida* populations in northern Europe have stickier eggs than populations from the south of Europe. This geographic pattern appears to result from variation in the distribution of their hosts. In the north, *A. tabida* is primarily a parasitoid of *Drosophila subobscura*, which appears to be unable to encapsulate parasitoids. In the south, *D. subobscura* is rare or absent, and *D. melanogaster* (which can encapsulate) is the main host.

Host specialization in parasitoids

Some parasitoids are generalists, attacking a wide range of host species, while others are more specialized, attacking one or a few closely related host species. Why should parasitoids become specialized, given that it reduces the number of potential hosts that they can oviposit in? One possible explanation is that, by specializing, they are able to forage for hosts more efficiently. This increase in foraging efficiency could be enough to compensate for the decrease in number of hosts attacked. Empirical evidence for this mechanism is lacking. Another possibility is that specialization allows parasitoids to develop more sophisticated counter-defences aimed at a specific host species.

However, the results described earlier in this section suggest that host defences and parasitoid counter-defences are very general, and so are likely to lead to more diffuse coevolution between groups of species. Supporting evidence for this comes from experiments that have shown that *D. melanogaster* lines selected for increased larval resistance to the parasitoid *Leptopilina boulardi* also showed increased resistance to the parasitoids *A. tabida* and *Leptopilina heterotoma*. The increase in resistance to *A. tabida* was similar in magnitude to that shown by lines selected for resistance to *A. tabida*. These support the importance of a general mechanism such as increasing haemocyte number.

Given such results it can be hard to see any advantage that could come from host specialization. However, lines selected against *A. tabida* showed increased resistance to *L. heterotoma*, but only a slight increase in their ability to survive attack by *L. boulardi*. A major difference between these species is that *A. tabida* and *L. heterotoma* are generalists, attacking many *Drosophila* species, while *L. boulardi* is a much more specialized parasitoid, attacking only *D. melanogaster* and a few very closely related species. This specialization could have allowed *L. boulardi* to evolve more specific adaptations. Consequently, the *D. melanogaster* lines selected against this species could have gained increased resistance through a specific defence mechanism against the specific parasitoid. Overall, the importance of both generalist and specialist defence and counter-defence mechanisms is supported.

Parasitoids and Population Dynamics

Understanding host–parasitoid population dynamics is important because of the clear

implications for biological control, but also because they have become a model system for investigating questions of resource–consumer dynamics (Jones *et al.*, 1994). The earliest models of host–parasitoid interactions often showed unstable equilibrium around which the populations oscillate with ever-increasing amplitude. Consequently, a major focus in the study of host–parasitoid dynamics has been what factors promote the stability of the interacting populations. A key component in this has been the effects of heterogeneous environments in which hosts and parasitoids are spatially distributed. In particular, parasitoid aggregation at certain patches has been suggested as an important factor in stabilizing host–parasitoid interactions. *See also: Population dynamics: introduction*

Parasitoid aggregation

Parasitoid aggregation may occur for two reasons. First, parasitoids may aggregate in patches of high host density; and secondly, parasitoids may aggregate in certain patches irrespective of high host density. These two types of parasitoid aggregation have been termed host density dependent (HDD) and host density independent (HDI).

Parasitoid aggregation is stabilizing because it leads to competition between individual parasitoids for hosts and a reduction in the average parasitoid searching efficiency. The reduction in the average parasitoid searching efficiency caused by aggregation increases as the average parasitoid density increases, and so introduces temporal density dependence into the system, which can stabilize the host–parasitoid interaction. Statistical methods exist for using field data on parasitism rates to estimate the relative importance of HDD and HDI in stabilizing population dynamics: while both can be important, HDI appears to play a larger role.

Space and individuals

More recently, more complex models have been created incorporating a range of biological details that have been suggested to influence the stability of host–parasitoid dynamics. Several studies have shown that facultative behaviour of searching parasitoids can lead to density dependence for a number of reasons such as variation in offspring sex ratio, interference, how individuals distribute themselves across patches, and variation in host defence and parasitoid counter-defence measures.

Another approach has been to consider spatially divided patches, between which there is some movement of individuals to nearby patches (a metapopulation). Not only can this stabilize population dynamics that are locally unstable, but it can lead to a range of complex spatial patterns such as spiral waves, spatially chaotic variation, and ‘crystal lattice’ patterns (Hassell *et al.*, 1991). *See also: Delete 128*

Multispecies systems and community dynamics

Most studies of host–parasitoid dynamics have concentrated on a single host species interacting with a single parasitoid. However, there have been a number of studies that have investigated larger numbers of interacting species (Jones *et al.*, 1994). These studies have shown a much wider and more complex range of dynamics than in simpler systems, and they are not necessarily just a simple blend of the separate pairwise interactions.

One area of particular interest that has attracted much theoretical and empirical interest is the apparent (indirect) competition that may arise when two hosts share a single generalist parasitoid, but do not compete for resources. In this case one host can drive the other host to extinction, as has been shown both theoretically and empirically (Bonsall and Hassell, 1997). Ultimately, the importance of such interactions and community dynamics will be determined by the relative importance of different types of interactions. Our knowledge of this will be determined by the construction of quantitative parasitoid webs, a topic that was considered earlier in this article.

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