Parasitoids

Behavioral and Evolutionary Ecology

H.C.J. GODFRAY

MONOGRAPHS IN BEHAVIOR AND ECOLOGY

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This book is dedicated to Caroline Elmslie

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Parasitoids

I cannot persuade myself that a beneficent and omnipotent God would have designedly created the Ichneumonidæ with the express intention of their feeding within the living bodies of Caterpillars, or that a cat should play with mice. Not believing this, I see no necessity in the belief that the eye was expressedly designed. On the other hand, I cannot anyhow be contented to view this wonderful universe, and especially the nature of man, and to conclude that everything is the result of brute force. I am inclined to look at everything as resulting from designed laws, with the details, whether good or bad, left to the working out of what we may call chance. Not that this notion at all *satisfies me. I feel most deeply that the whole subject is too profound for the human intellect. A dog might as well speculate on the mind of Newton. Let each man hope and believe what he can.*

—Charles Darwin
22 May 1860, Letter to Asa Gray

1

Introduction

Alien, a very popular motion picture of 1979, described the fate of the occupants of a spaceship infiltrated by a deadly alien life form. Larvae of these creatures entered the bodies of the crew where they developed and grew, their eventual emergence resulting in the (spectacular) death of the infected human. Why did this film achieve such widespread popularity (as I write, *Aliens 3* is about to be released)? An imaginative script, an attractive star, and the survival of the ship's cat certainly helped, but possibly also the assurance that the events depicted could not happen on earth. This is certainly true for humans: many of us are plagued by parasites, but by nothing quite as gruesome as this. Yet the creature in *Alien* is immediately recognizable as a parasitoid—specifically a primary, solitary, endoparasitoid with a planidial larva—differing in minor detail (no DNA, silicon-based biochemistry) from thousands, possibly millions, of species of insects that attack other arthropods in nearly every terrestrial ecosystem. This book is about the behavioral and evolutionary ecology of earth-based parasitoids.[1]

Parasitoids are insects whose larvae develop by feeding on the bodies of other arthropods, usually insects. Larval feeding results in the death of the parasitoid's host. Although the natural history and identity of parasitoids are little known among nonbiologists, they are of immense importance in natural and agricultural ecosystems where they influence or regulate the population density of many of their hosts. Much research on parasitoids has been stimulated by their frequent success in biological control programs; many species have been released to combat agricultural pests, and while effective control is by no means assured, huge savings, both in financial and human terms, have resulted from successful programs.

Research on the parasitoids of agricultural and other pests has generated a huge amount of information on the behavior and ecology of many different species. In addition there is a large and increasing number of studies of the fundamental biology of parasitoids. In this book, I attempt to review recent research on parasitoid behavioral and evolutionary ecology. I aim to show that parasitoids provide marvelous systems for investigating outstanding problems in behavioral and evolutionary ecology, and that fundamental research can

[1] Thus I exclude discussion of the mutational response of the braconid wasp *Bracon hebetor* (=*Habrobracon juglandis*) in the Biosatellite II experiment (von Borstel et al. 1968).

illuminate many aspects of parasitoid biology that are important to applied entomologists.

My approach to many of the evolutionary questions discussed in this book is that of modern behavioral ecology. This research program is often the subject of criticism, both fair and unfair, and a brief word is needed to explain my use of the method. Natural selection is an optimization process that tends to maximize the efficiency with which genes are transmitted to future generations. This property of natural selection can be used to make predictions about the morphology, physiology, or behavior of animals or plants. The behavioral ecologist attempts to understand how animal behavior interacts with the environment to determine fitness. He or she tries to distinguish the behavioral options available to the animal (the strategy set), the consequences for the animal of adopting different strategies, and how the consequences translate into Darwinian fitness. These hypotheses constitute a model of animal behavior, and the optimizing property of natural selection is used to make the prediction that the behavior observed in the field is that which maximizes fitness. What is at test is not the assumption that the animal is behaving optimally—that is axiomatic—but the model of animal behavior.

Use of the behavioral ecological method has led to great insights into animal behavior, and I hope to convince the reader that some of the best examples of this technique are provided by studies of parasitoids. Nevertheless, there are potential pitfalls. Problems begin when animals fail to conform to predicted behavior. There are at least two potential explanations for this failure. First, the model of animal behavior may be incorrect. The manner in which the test failed often provides useful information about important aspects of the animal's biology that have been omitted from the model. Typically, the model is revised, and a new prediction made; ideally, the revised prediction is tested with a new experiment. Successive iteration can be a valuable way of dissecting the functional significance of animal behavior; however, there is also a danger of overinterpretation—of making a posteriori modifications to the model to force it to fit the facts. It is important to distinguish between new ideas stimulated by a failed test, and hypotheses that have been subject to independent experiments. The second explanation for a failed test is that the underlying assumption that the animal is behaving optimally is untrue. Perhaps the animal has not yet had time to adapt to the environment, or perhaps the mechanics of the genetic process prevent sufficiently good adaptation. There are no general solutions to these problems, and biologists working within the behavioral ecological research program must be constantly aware of these potential difficulties.

A recurring problem in behavioral ecology is understanding how different behaviors affect Darwinian fitness. Typically, a surrogate measure of fitness is used; for example, in studies of foraging behavior, it is often assumed that the foraging strategy that maximizes the rate of energy intake also maximizes fitness. The study of many aspects of parasitoid reproductive strategy is simplified by a very direct link between behavior and fitness: the consequences of failing to find a host, or making an incorrect oviposition decision after locating a host, are obvious and relatively easy to measure. This simplicity makes parasitoids an important model system in the development of behavioral ecological methods.

In my discussion of behavioral ecological hypotheses, I sometimes use an informal shorthand and write, for example, that a parasitoid seeks to locate as many hosts as possible, or to lay a clutch size that maximizes the number of offspring that can develop on a host. Such phrases do not of course imply any conscious motivation or calculation on the part of the parasitoid, but just avoid the constant repetition of long sentences detailing precisely how natural selection is assumed to maximize fitness.

Many aspects of parasitoid behavior have both an evolutionary and a mechanistic explanation. Consider the question of the relationship between clutch size and host size in gregarious parasitoids. In chapter 3 I describe behavioral ecological models designed to predict the optimal clutch size on hosts of different size. These models attempt to provide an ultimate or evolutionary explanation for clutch size behavior. At a different level, questions can be asked about the behavioral mechanisms responsible for clutch size. For example, what properties of the host cause the parasitoid to lay a particular number of eggs? It is important not to fall into the trap of treating answers to evolutionary "why" questions and mechanistic "how" questions as alternatives: they are instead complementary. Indeed, one of the most interesting challenges in modern behavioral ecology is to dissect the behavioral rules that allow an animal to pursue behavioral strategies favored by natural selection. Work with parasitoids is likely to be important in exploring this problem, both because of the straightforward link between behavior and fitness, and also because many oviposition decisions faced by parasitoids are relatively simple and amenable to experimental manipulation. There are of course other levels of questions that might be asked about behavior in addition to the evolutionary and mechanistic—for example, questions about the neurological or hormonal basis of behavior.

The rest of the chapter is organized as follows. The next section deals with different definitions of the term "parasitoid" while the following reviews the main features and variants of parasitoid life histories. The study of parasitoids has generated its fair share of specialist terminology, and although an attempt has been made to use as little jargon as possible, a minimal set is introduced in this section. The third section describes the natural history of a few more specialized forms of parasitoids that will be referred to later in the book. The fourth section comprises a brief overview of parasitoid taxonomy, while the fifth section discusses the origins of the parasitoid habit and describes the natural history of groups that have evolved from parasitoids.

1.1 Parasitoid Definitions

A parasitoid is defined by the feeding habit of its larva. The larva feeds exclusively on the body of another arthropod, its host, eventually killing it. Only a single host is required for the parasitoid to complete development, and often a number of parasitoids develop gregariously on the same host. In many ways parasitoids are intermediate between predators and parasites: like predators, they always kill the host they attack; like many parasites, they require just a single host on which to mature. After attacking a host, the female parasitoid does not attempt to move the host to a prepared cache or nest. This distinguishes parasitoids from some solitary wasps which in other respects they closely resemble. The life cycle of all parasitoids can be divided into four stages—egg, larva, pupa, and adult—in other words, they belong to the holometabolous insect orders.

Although the term "parasitoid" was introduced by Reuter in 1913, it is only in the last twenty years that it has become universally accepted. Before that, parasitoids were most commonly referred to as insect parasites. Understandably perhaps, the clumsy words "parasitoidize" and "parasitoidism" have never found favor, and I shall follow normal practice and use "parasitize" and "parasitism." The term "protelean parasite" is sometimes used both to refer to parasitoids and to insects that are true parasites in their larval stage (e.g., Askew 1971). Flanders (1973) attempted, without success, to replace "parasitoid" with "carniveroid."

Several authors have attempted to expand parasitoid to include other organisms with related life histories. Eggleton and Gaston (1990) argued that the term should be used for all organisms that complete their development on, and then kill, a single animal host. This definition includes solitary wasps, and organisms as diverse as fungi and nematodes. Price (1975), on the other hand, accepts that parasitoids are insects but allows their hosts to be plants; seed weevils (Bruchidae) whose larvae develop on and kill a single seed are thus included in this definition. These authors are making important points about organisms with similar trophic functions and adaptations. Nevertheless, I prefer to retain the term "parasitoid" in its more restricted sense, both because this is the sense in which it is used by most biologists, and because parasitoids, defined in this way, are faced with a multitude of similar biological problems that they have to solve in order to survive.

According to Silvestri (1909), the first published observation of a parasitoid emerging from a host was by U. Aldrovandi in 1602, and the first illustration was that of Johannes Goedaert in 1662. Apparently neither author fully understood his observations. Silvestri credits Antonio Vallisnieri for the first correct interpretation of insect parasitism in 1706, but DeBach (1974) says that van Leeuwenhoek in 1701 correctly described the parasitism of a willow sawfly. John Ray, however, in 1710 published an account of parasitism of white butterflies by what is now called *Cotesia (=Apanteles) glomeratus* based on observations made in 1658 (Mickel 1973; Shaw 1981b). Whoever may have first understood the parasitoid life cycle, its true nature became widely known in entomological circles in the first half of the eighteenth century.

1.2 Parasitoid Natural History

The free-living adults of parasitoids generally look much like their closest nonparasitoid relatives (fig. 1.1). Hosts are usually located by the adult female who lays her eggs either directly on the host or in its immediate vicinity. Hymenopteran parasitoids have highly specialized ovipositors which are used both to manipulate eggs and to sting the host. The sting causes paralysis that may be permanent, or the host may recover and continue feeding. Parasitoids that attack concealed hosts often have long ovipositors which, when not in use, either extend beyond the end of the abdomen enclosed between protective valves, or are coiled inside the abdomen of the female. Cutting ridges at the end of the ovipositor allow wasps to drill through plant tissue and even wood to locate hidden hosts. In exceptional cases, the ovipositor can be eight times the length of the rest of the body (Askew 1971). Special adaptations are needed to allow the egg to pass down long and thin ovipositors; often the egg is very small and expands enormously within the host's body. In a number of hymenopteran and dipteran parasitoids the whole abdomen is laterally or dorsoventrally compressed so that it can be slid into narrow openings, for example to locate hosts between the gill slits of fungi. Adult parasitoids may feed from flowers, sap fluxes, and other energy sources, and many also feed on potential hosts (*host feeding*).

In some cases, the adult female does not lay her eggs on the host but on the host's foodplant. Parasitism occurs if the host eats the eggs. There are also some parasitoids that lay their eggs away from the host but which have active free-living first instar larvae that are responsible for host location (sec. 2.2.5).

The hosts of parasitoids are almost exclusively insects themselves, although spiders and even centipedes are occasionally parasitized. The juvenile stages of insects are most frequently attacked, although a few groups attack adult insects. The parasitoids of holometabolous insects such as Lepidoptera, beetles, and flies can be classified by the stage they attack. Thus a host may suffer attack from *egg parasitoids, larval parasitoids, pupal parasitoids*, or *adult parasitoids*. Some parasitoids lay eggs in one host stage but their progeny do not kill the host until it has entered a later stage, for example *egg-larval* and *larval-pupal parasitoids*. Hemimetabolous insects (with no pupal stage) are also attacked by egg parasitoids, but there is less of a distinction between parasitoids attacking nymphal and adult stages.

Parasitoids can be divided into two classes by the feeding behavior of their larvae. Some parasitoids develop within the body of their host, feeding from

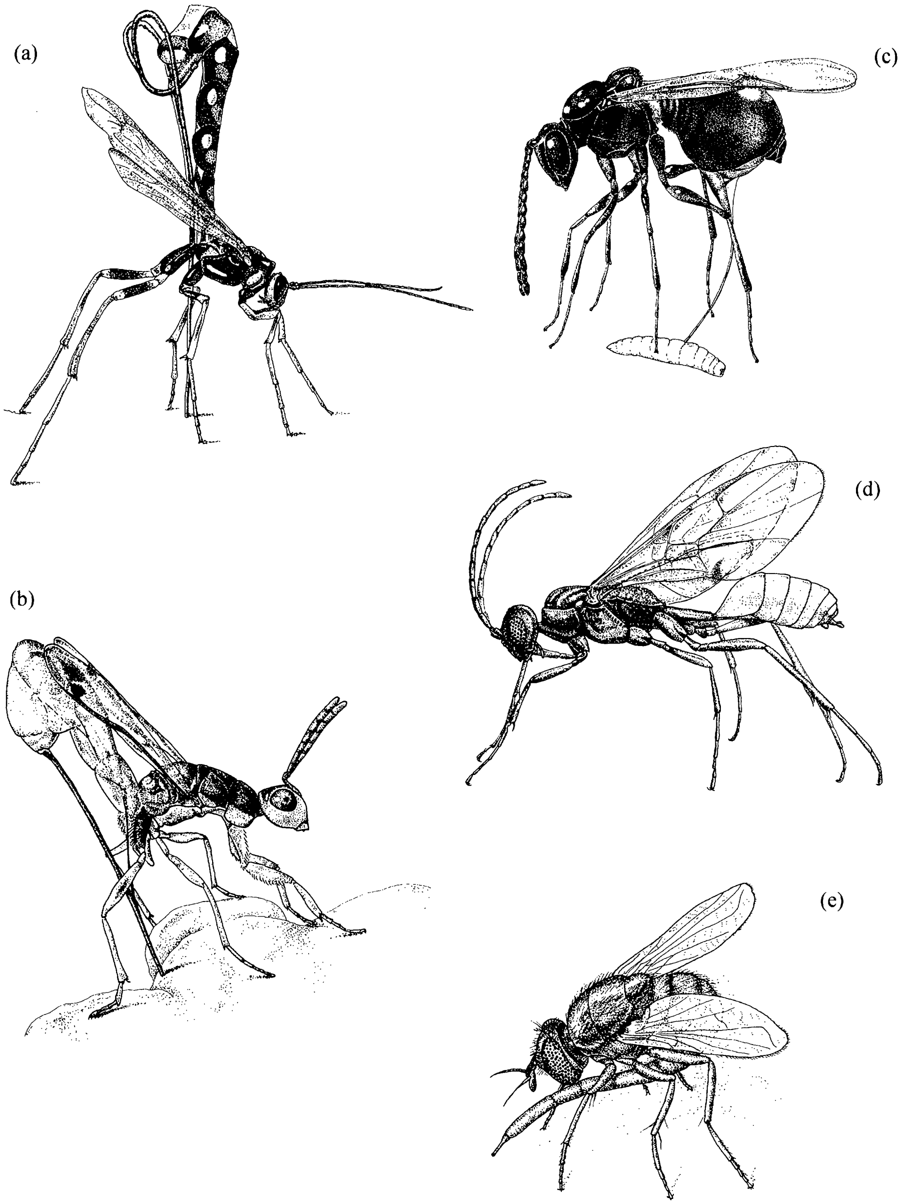

Figure 1.1 The adults of some of the main taxonomic groups of parasitoids. Insects (a)–(d) are Hymenoptera, and (e) is Diptera: (a) *Megarhyssa* sp. (Ichneumonoidea: Ichneumonidae) ovipositing into a concealed larva in wood; after a photograph in Gauld and Bolton 1988; (b) *Megastigmus stigmatizans* (Chalcidoidea: Torymidae) ovipositing into a cynipid gall; from a photograph taken by Graham Stone; (c) *Leptopilina clavipes* (Cynipoidea: Eucoilidae) attacking a *Drosophila* larva; from a photograph taken by Marcel Visser; (d) *Xiphyropronia tianmushanensis* (Proctotrupoidea: Roproniidae) after He and Chen 1991; (e) *Nemorilla floralis* (Tachnidae) about to oviposit; after Herting 1960.

the inside, and are known as *endoparasitoids. Ectoparasitoids*, on the other hand, live externally, normally with their mouthparts buried in the body of their host. The majority of parasitoids fall naturally into one of these groups though there are a minority of species that spend their first few instars as ectoparasitoids before burrowing into their hosts to become endoparasitoids, or vice versa.

Parasitoids that feed alone on a host are known as *solitary* parasitoids as opposed to *gregarious* parasitoids, where from two to several thousand individuals feed together on a single host. If further eggs are deposited on the host by the same species of parasitoid, *superparasitism* is said to occur. If a second female of a different species lays her eggs on the host, one of two things may happen. If the larvae of the second species compete with the resident larvae for host resources, *multiparasitism* occurs. However, if the larvae of the second species feed, not on the host, but on the parasitoid larvae already present, *hyperparasitism* occurs. Hyperparasitism is generally of two kinds: *facultative hyperparasitoids* are able to attack unparasitized host individuals and only develop as hyperparasitoids when eggs are laid on a previously parasitized host; in contrast *obligate hyperparasitoids* are only able to develop as parasitoids of parasitoids. Hyperparasitoids are often referred to as *secondary parasitoids* and cases are even known of *tertiary parasitoids.* A final, rather rare type of parasitism is *cleptoparasitism.* A cleptoparasitoid obligatorily requires the presence of another species of parasitoid, though, unlike a hyperparasitoid, does not feed on it. Good examples of cleptoparasitism are certain parasitoids of insects living inside dead wood that lack a boring ovipositor and which can only attack previously parasitized insects after the first parasitoid has drilled a hole for oviposition (Spradbery 1969).

Parasitoids that allow hosts to continue to grow in size after parasitism are called *koinobionts* as opposed to *idiobionts*, where the parasitoid larvae must make do with the host resources present at oviposition (Haeselbarth 1979; Askew and Shaw 1986). Egg, pupal, and adult parasitoids are usually idiobionts, as are those larval parasitoids whose sting causes permanent paralysis. The most important types of koinobionts are egg-larval and larval-pupal parasitoids, and those larval parasitoids which do not permanently paralyze their host at oviposition. Koinobiont parasitoids normally suspend their development as first instar larvae while the host continues to feed and grow, or they begin to grow but refrain from feeding on the vital organs of their host.

There is much variation in pupation site among parasitoids. Egg, pupal, or larval-pupal parasitoids usually pupate within the egg or pupa of the host, taking advantage of the relative security of one of the host's more protective stages. Species attacking hosts such as moth larvae or aphids frequently cement the eaten-out husk of the host to the substrate and pupate within this shelter, usually referred to as a *mummy*. Parasitoids of hosts living within galls, mines, or in other concealed habitats often form naked pupae near the remains of the host. Parasitoids of hosts that feed in exposed situations usually pupate within protective cocoons of silk produced by the larvae themselves. The pupae of some wasps hang suspended on a silken thread from a leaf or other substrate. Where parasitoids have several generations a year and overwinter in the pupal stage, the winter cocoon is often considerably thicker and tougher than cocoons made during the summer.

There are several books that provide very good introductions to parasitoid biology. Askew's (1971) excellent book, *Parasitic Insects*, provides a wealth of interesting biological and natural history detail and also deals with true parasites such as fleas, lice, and biting flies. Gauld and Bolton's (1988) *Hymenoptera* surveys the order from a taxonomic viewpoint but includes much biology and natural history. Oldroyd's (1964) *Natural History of Flies* includes a good introduction to fly parasitoids. Though now rather dated, Clausen's (1940a) classic, *Entomophagous Insects*, provides an encyclopedic compendium of parasitoid biology. Finally, the edited volume by Waage and Greathead (1986) contains an important series of reviews on many aspects of parasitoid biology.

1.3 Unusual Life Histories

Several groups of parasitoids with unusual or bizarre life histories provide interesting tests of evolutionary hypotheses. As they will be referred to in several places in the book, their natural history and biology are described here to avoid unnecessary repetition.

1.3.1 POLYEMBRYONIC PARASITOIDS

One of the most spectacular sights in parasitoid biology is the emergence of 2000 small wasps from the eaten-out husk of a moth caterpillar. These wasps have arisen from the asexual division of one or two eggs laid by an adult female into the egg of the moth. This form of asexual division is called *polyembryony* and is known from four families of parasitoid wasps (Ivanova-Kasas 1972), each representing an independent evolutionary event. Outside parasitoids, polyembryony is found rarely and sporadically throughout the animal kingdom, from planarians to armadillos.

Polyembryony in parasitoids was first described by Marchal (1898) in the chalcidoid family Encyrtidae, where it is found in a series of closely related genera (tribe Copidosomatini) of egg-larval parasitoids of Lepidoptera. Recently, Strand and his colleagues have used a variety of modern techniques from physiology and molecular biology to investigate polyembryony in the encyrtid wasp *Copidosoma floridanum.* Here I provide a brief description of polyembryony in *C. floridanum* based on Strand's findings (1989a, 1989b, 1989c, 1992, pers. comm.).

A female *C. floridanum* lays either a single egg (male or female) or two eggs (always one male plus one female) into its host, the egg of a noctuid moth. The moth egg hatches into a larva which develops until its final instar. During this period, a single parasitoid egg can divide to produce up to 1500 separate individuals (3000 in related species). However, the host suffers no major ill effects of parasitism until its final instar, when the parasitoids develop quickly, consume the host, and then pupate within the skin of the exhausted caterpillar.

There are some subtle differences in the development of male and female eggs. Consider female eggs first. The egg initially appears to divide normally to produce a mass of similar-looking cells enclosed within a serosal membrane, derived from the polar bodies. In a normal parasitoid, the egg would then develop through a blastula and then a gastrula stage. In *C. floridanum*, the cell mass divides to produce a number of "daughter" masses, each contained within a membrane, the assemblage bounded by the original serosal membrane. The term "polygerm" is often used to describe the collection of individual cell masses and their associated membranes, while the maturing cell masses are called "morulae." As the host larva ages, the morula-stage embryos proceed through a number of rounds of division, perhaps synchronized by cycles of endocrine hormones associated with the progression of host instars. In the last instar, again triggered by changes in host hormone titres (Strand et al. 1989, 1990, 1991a, 1991b), the now numerous embryos embark on a normal path of development.

Early embryologists noted that a few embryos began development very much earlier than the majority, and that they developed into atypical larvae with relatively large mandibles that eventually died (Silvestri 1906). Cruz (1981) proposed that the function of these larvae was to protect their (genetically identical) siblings from competition from other parasitoids. Female eggs typically produce five to eight defensive larvae during the early stages of morula division. The mechanism that allows only a few embryos to develop precociously is not yet known. Interestingly, artificial elevation of host juvenile hormone titer or starvation of the host increases the number of defensive larvae produced.

The development of male eggs is similar except that instead of developing in the anterior of the host larva, they develop more posteriorly, associated with the host fat body. Male eggs also produce defensive larvae, but far fewer, and only when the host larva is quite large.

Polyembryonic species of other families of wasps do not produce the very large broods found in some encyrtids. The Platygastridae are a rather poorly known family of parasitoid wasps that attack a variety of hosts, especially cecidomyiid gall midges. It is thought that a number of species in the genus *Platygaster* are polyembryonic, though it appears that the female deposits several eggs in each host, not all of which need divide polyembryonically. The maximum number of individuals emerging from a single host is about twenty. A rather large, and sometimes contradictory, early literature on platygasterid development is reviewed by Clausen (1940a); there seem to be no modern investigations. Polyembryony is known from some members of the braconid genus, *Macrocentrus*, egg-larval parasitoids of lepidopterans. Again, an undifferentiated mass of cells divides to form up to about forty embryos (Voukassovitch 1927; Parker 1931). In one species, *M. ancylivorus*, development initially proceeds as in polyembryonic species, but when one individual reaches the larval stage, it appears to inhibit further development by its siblings (Daniel 1932). If two individuals develop simultaneously, they fight until just one survives. There is some evidence for a similar form of incipient polyembryony in *Platygaster* (Clausen 1940a). The Dryinidae are parasitoids of planthoppers (Auchenorrhyncha) and one species is known to be polyembryonic: the aberrant *Crovettia (=Aphelopus) theliae* is an endoparasitoid of membracid nymphs and one egg divides to produce up to seventy larvae (Kornhauser 1919).

1.3.2 HETERONOMOUS APHELINIDS

In most parasitoids, male and female progeny develop on the same type of host. Quite often, male eggs tend to be laid on smaller hosts and female eggs on larger hosts (see Section 4.4), but at least potentially either sex can develop on large and small hosts. The chalcidoid family Aphelinidae is unique in containing many species where the two sexes are obligatorily restricted to developing on different types of host (Viggiani 1984), a feature first described by Flanders (1936). The female wasp always develops as an endoparasitoid of a homopteran, for example a mealy bug, scale insect, or whitefly, while the site of development of the male is variable. Walter (1983a, 1983b) coined the term *heteronomous aphelinids* for species with sexually dimorphic development, and distinguished three main types of life history (this classification has largely superseded earlier systems by Flanders 1959, 1967; Zinna 1961, 1962; and Ferrière 1965).

Diphagous parasitoids. Males develop, like females, as parasitoids of homopterans but as ectoparasitoids, rather than endoparasitoids. Here the mode of development differs between the sexes, but not the type of host.

Heteronomous hyperparasitoids (sometimes called autoparasitoids or adelphoparasitoids). Males develop as hyperparasitoids of homopterans, attacking females of their own or another species of parasitoid. Heteronomous hyperparasitoids vary in the range of parasitoid species suitable for male development; Walter (1983a) suggests some wasps always avoid, and others are restricted to, females of their own species. Some species only place male eggs in homopterans already containing a suitable female host while others lay male eggs in unparasitized homopterans even though they will only survive if a second wasp places a female egg in the same insect. Finally, the male egg may develop either as an endoparasitoid or an ectoparasitoid of a female larva.

Heterotrophic parasitoids. Males develop on completely different hosts: the eggs of Lepidoptera. However, in a review of egg parasitism by Aphelinidae, Polaszek (1991) has recently questioned whether males of these species are in fact obligate parasitoids of lepidopteran eggs and concludes that heterotrophic parasitism is "a phenomenon which, in all probability, does not exist."

How might heteronomy have evolved? Walter (1983a) points out that in some species of nonheteronomous Aphelinidae, where both males and females develop as primary endoparasitoids of homopterans, the oviposition site of male and female eggs is subtly different. For example, *Aphytis melinus*, a parasitoid of red scale (*Aonidiella aurantii*), lays female eggs on the dorsum of the host, beneath the scale cover, while male eggs are laid under the scale-insect's body (Abdelrahman 1974; Luck et al. 1982; curiously, the related *A. lignanensis* lays male and female eggs in both positions). The explanation of this behavior is not known, but once male and female eggs are deposited in different sites, genes with sex-limited expression might allow the development of the two sexes to evolve independently. Walter (1983a) suggests that diphagous parasitoids evolved first as this life history involves little change in the behavior of the adult wasp. Once diphagy was established, the adult female wasp might be selected to adjust her behavior leading to the other forms of heteronomous parasitism.

1.3.3 Fig Wasps

There are about eight hundred species of fig (Moraceae, *Ficus*), the majority trees but also climbers and shrubs, distributed throughout the tropics with a few temperate species (including the edible fig). All sexual fig species are pollinated by chalcidoid wasps in the family Agaonidae which develop as mutualists in galls within the fig. With a few possible exceptions, every species of fig has its own species of pollinating wasp. Pollinating fig wasps are not parasitoids although they have certainly evolved from parasitoids. However, the larvae of pollinating fig wasps are attacked by other species of fig wasps that are true parasitoids. The bizarre life history of many fig wasps has attracted much attention by evolutionary biologists. Because the biology of fig wasp pollinators and parasitoids is so interwoven, both types of insects are considered here. For recent studies of fig wasp biology and an entry into the earlier literature, see Hamilton (1979), Janzen (1979); Boucek et al. (1981), Frank (1984); Kjellberg and Valdeyron (1984); Herre (1985, 1987, 1989); Kjellberg et al. (1987); Murray (1985, 1987, 1989, 1990); Godfray (1988); Bronstein (1988a, 1988b); and Grafen and Godfray (1991).

The flowers of the fig plant line the inside walls of the hollow fig "fruit," or syconium. When the fig is young, female pollinators crawl into the central cavity through a small pore or ostium. The pore is so narrow that wasps frequently lose wings, legs, or antennae and they never again leave the fig. Fig trees may be either monoecious or dioecious. The figs of monoecious species contain three types of flowers: male flowers, female flowers that if fertilized develop into seeds, and female flowers that support the development of a fig wasp. Dioecious fig trees may be either male or female: the figs on male trees contain male flowers and female flowers capable of supporting fig wasps, while the figs on female trees only contain female flowers from which seeds will develop (as "male" figs contain female flowers, albeit not flowers from which seeds will develop, dioecious species should strictly be called gynodioecious). Once inside the fig, the female pollinating wasp seeks to lay her eggs in flowers that support the development of her offspring. While ovipositing, she pollinates the female flowers using pollen that has either adhered to her body, or that she collected and placed in special receptacles on her body before leaving the fig in which she was born. Note that in dioecious fig trees, wasps that enter female figs fail to produce any offspring.

The young fig wasp develops on the fleshy endosperm within the female flower. As the fig grows, the pore closes and the insects are completely isolated from the outside world. The males and females of the pollinating fig wasps are extraordinarily sexually dimorphic. The adult female has a fairly typical chalcidoid appearance, though the face is characteristically projected forward. The male is a very curious insect. All traces of wings and pigmentation have disappeared and the compound eye is reduced to a few ommatidia; the abdomen is long and tubular and often reflexed underneath the body. The male never leaves the fig and its strange morphology can be viewed as an adaptation to its sole aim in life, that of finding and inseminating females in the dark world of the interior of the fig. Typically, males emerge from the pupae first and roam through the fig until they find a gall containing a female. They chew through the wall of the gall and then insert their tubular abdomen, inseminating the female prior to her emergence. When the females hatch, they collect pollen from the male flowers and leave the fig. Sometimes the pore reopens, allowing the females to escape, while in other species the male wasps dig a hole through the side of the fig.

A variety of species parasitizes the mutualism between fig and fig wasp. Some agaonids have identical life histories to the pollinating wasps except that they carry no pollen. As the endosperm required for the developing larva develops after pollination, individuals of these wasps can produce offspring only in figs that have also been entered by the legitimate pollinator, with which they compete for resources. Other species of wasps lay their eggs in the gall flowers without ever entering the fig. A large and diverse group of wasps traditionally placed in the family Torymidae[2] are characterized by extremely long ovipositors which they use to pierce the wall of the fig and to lay an egg in a gall containing a developing fig wasp. The larva of the wasp develops as a parasitoid of the fig wasp though also probably feeds on plant tissue. While Torymidae are the most common parasitoids of the pollinators, a few other chalcidoid groups have also evolved to parasitize the mutualism. Some pteromalids lay their eggs into developing gall flowers although, unlike the Torymidae, these insects often enter the fig to oviposit.

The females of nonpollinating fig wasps tend to resemble typical chalcids

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[2] The taxonomic status of these species is controversial. Traditionally placed in the Torymidae (subfamily Idarninae), Boucek (1988) has recently argued that they are more properly placed with the true fig wasps in the family Agaonidae.

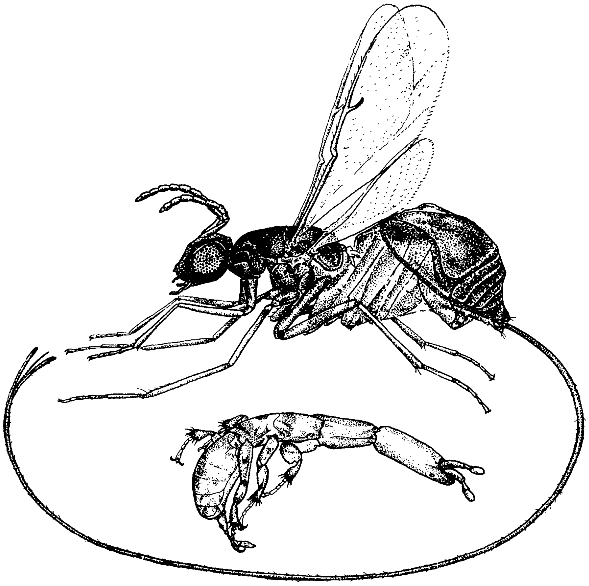

Figure 1.2 Male (lower) and female (upper) of the parasitoid figwasp *Apocrypta perplexa* (Chalcidoidea: Torymidae). After Ulenberg 1985.

except that species which lay eggs from the outside of the fig have extremely long ovipositors. The males of some species never leave the fig and have developed extremely specialized morphologies, often paralleling the adaptations of the pollinating wasps (fig. 1.2). As discussed further in sec. 7.2.1, some species have evolved fearsome mandibles and fight among themselves for the privilege of mating the conspecific females in the fig. The males of other species are similar to females, while yet other species have two types of male: normal males that leave the fig and highly modified males that compete for mates within the fig (see sec. 7.2.1).

1.3.4 AQUATIC PARASITOIDS

A few parasitoids have become adapted to attack aquatic and semiaquatic hosts. The eulophid *Mestocharis bimaculatus* parasitizes water beetle eggs, but only when exposed by fluctuating water levels. It can walk on the surface film but drowns if fully submerged (Jackson 1964). The mymarid *Caraphractus cinctus* and the trichogrammatid *Prestwichia aquatica* also attack the eggs of water beetles and other freshwater insects. These species are fully aquatic, using their wings and legs respectively as oars (Lubbock 1862; Jackson 1958; Askew 1971). They are minute insects, which probably allows them to obtain sufficient oxygen by diffusion across the surface of their bodies. The much larger ichneumonid *Agriotypus armatus* searches for caddis larvae under water: it is able to stay submerged for thirty minutes using oxygen in air trapped in the thick pubescence that clothes its body. Before pupating, the wasp's larva constructs a rigid ribbon of silk containing a bubble of air which acts as a plastron supplying the pupa's oxygen needs (Askew 1971).

1.4 Parasitoid Taxonomy

The majority of parasitoids are either members of the order Hymenoptera (the sawflies, ants, bees, and wasps) or the order Diptera (true flies). There are probably about 50,000 described species of hymenopteran parasitoids (Gaston 1991; LaSalle and Gauld 1991), 15,000 described species of dipteran parasitoids, plus about 3,000 species in other orders (Eggleton and Belshaw 1992), giving a grand total of about 68,000 described species. In all there are between 750,000 and 850,000 described species of insects (Gaston 1991) so parasitoids constitute about 8.5% of all insects (and a little over 4% of all metazoans). There is considerable debate about the total number of described and undescribed species of insects although there is most support for a figure of around 8 million (Gaston 1991). If parasitoids make up the same proportion of described and undescribed species, then there are around 800,000 species of parasitoid. However, many workers argue that parasitoids are relatively poorly known. LaSalle and Gauld (1991) suggest that parasitic Hymenoptera alone might constitute up to 20% of all insects, and Crosskey (1980) states that the Tachinidae, the large family of dipteran parasitoids, may be the most species-rich family of flies. Assuming that parasitoids constitute 20%–25% of the 8 million species of insects, these estimates put an upper bound of around 1.6–2 million on the number of species of parasitoid on earth.

1.4.1 HYMENOPTERA

The great insect order Hymenoptera is divided into two suborders, the Symphyta and the Apocrita. The Symphyta contains the sawflies, a primarily phytophagous group of insects though it contains a few species of parasitoids. The Aprocrita comprises the ants, bees, and wasps and is itself split into two major divisions, the Parasitica and the Aculeata. As their name suggests, the Parasitica are almost exclusively parasitoids. Most species in the Aculeata are predatory or collect pollen, but a few species are parasitoids. The eusocial Hymenoptera all belong to the Aculeata.[3]

Table 1.1 summarizes the taxonomy of hymenopterous parasitoids and lists the families mentioned in this book with some estimates of their relative abun-

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[3] Unfortunately, the divisions of the Hymenoptera outlined here cannot be justified as part of a phylogenetic (cladistic) classification. A valid taxon must be holophyletic, that is, have a single evolutionary origin (monophyly) and contain all descendant species. The Symphyta is mono-

Table 1.1
Families of Hymenoptera containing parasitoids and mentioned in the text, and the number of representatives in the British fauna, in a large collection from Sulawesi (Indonesia), and in the estimated number of described species in the world fauna.

Suborder ***Division*** *Superfamily* Family	*British Fauna*[a]	*Sulawesi Fauna*[b]	*World Fauna*[c]
Symphyta			
Orussoidea			
Orussidae	1	†	75
Apocrita			
Parasitica			
Trigonalyoidae			
Trigonalyidae	1	†	70
Evanoidea			
Evaniidae*	2	15	400
Aulacidae	1	†	150
Gasteruptiidae	5	†	500
Cynipoidea			
Ibaliidae	2	†	9
Figitidae	34	3	125
Eucoilidae	55	365	1000
Charipidae	39	†	1200
Chalcidoidea			
Leucospidae	0	†	139
Chalcididae	7	†	1500
Eurytomidae	89	26	1100
Torymidae	74	14	1500
Agaonidae [Fig Wasps]	0	50	800
Eucharitidae	0	†	350
Perilampidae	9	†	200
Pteromalidae	528	115	3100

Table continues on following page

dance. Typical examples of adults of the major superfamilies are illustrated in figure 1.1.

The taxonomy of parasitoid Hymenoptera presents some of the greatest challenges facing systematic entomologists today. Even in regions with ex-

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phyletic but gave rise to the Apocrita and is thus paraphyletic. The Apocrita is generally considered holophyletic but the Parasitica is paraphyletic, since the Aculeata evolved from members of this group. Finally, the Aculeata are probably holophyletic. In the absence of any serviceable phylogenetic classification, nearly all authors are content to stick with the traditional classification. For a full discussion of these taxonomic problems, see Gauld and Bolton (1988).

Table 1.1 (*continued*)

Suborder ***Division*** *Superfamily* Family	*British Fauna*[a]	*Sulawesi Fauna*[b]	*World Fauna*[c]
Chalcidoidea (cont.)			
Signiphoridae	2	†	75
Encyrtidae	191	254	>3000
Aphelinidae	37	229	900
Eulophidae	382	484	>3000
Trichogrammatidae	29	51	532
Mymaridae	84	165	1300
Proctotrupoidae			
Proctotrupidae	36	12	334
Diapriidae	298	181	2028
Scelionidae	102	250	2768
Platygastridae	157	120	987
Roproniidae	0	0	17
Ceraphronoidae			
Megaspilidae	67	9	250[d]
Ceraphronidae	26	215	
Ichneumonoidea			
Ichneumonidae	2029	420	15000
Braconidae	1163	431	10000
Aculeata			
Chrysidoidea			
Dryinidae	44	16	850
Bethylidae*	20	55	2000
Chrysididae*	31	20	3000
Vespoidea			
Tiphiidae	4	7	1500
Pompilidae*	41	46	4000

* Family contains many species that are not true parasitoids. Numbers given refer to the total species in the family.

† Data not given: absent or very rare.

[a] Data from Noyes 1989, Gauld and Bolton 1988, and Fitton et al. 1978.

[b] Data from Noyes 1989.

[c] Estimated numbers of described species; data from Gauld and Bolton 1988, Gaston 1991, Lasalle and Gauld 1991, Vlug 1993, Johnson 1992.

[d] P. Desert (pers. comm.) estimates there are approximately 250 valid descriptions of Ceraphronidae but a very large number of both undescribed species and invalid names.

tremely well-known faunas, such as northern Europe, there are some genera and subfamilies in which it is not possible to identify reliably individual specimens at the species level. The chief reasons for this taxonomic intractability are the amount of variation commonly observed within species, the paucity of character states of use to the taxonomist, and the frequent occurrence of convergent evolution, parallel evolution, and character reversal (Gauld 1986a). Compounding the inherent difficulties with the group, the activities of the first generation of Hymenoptera systematists tended to increase the taxonomic confusion. Frequently unaware of intraspecific variation, nineteenth-century taxonomists, such as the legendary Francis Walker, described huge numbers of species. Untangling the nomenclatural chaos so created has been the life work of several of this century's most eminent taxonomists (e.g., Graham 1969). Gauld and Bolton (1988) provide an entry into the taxonomic literature.

1.4.2 DIPTERA

Traditionally, the true flies are divided into three suborders, the Nematocera (crane flies, midges, mosquitoes, etc.), the Brachycera (horseflies, robber flies, bee, flies, etc.), and the Cyclorrhapha (higher flies). The taxonomic subdivision of the Cyclorrhapha is quite complex but includes two major assemblages that contain parasitoids, the Acalypterae (a group containing many families with varied life histories) and the Calypterae (houseflies and relatives). Parasitoids are very rare in the Nematocera, but several important families of Brachycera, Acalypterae, and Calypterae are exclusively parasitoids. Table 1.2 lists

Table 1.2
Families of Diptera containing parasitoids and mentioned in the text, and the number of described species in the British and world faunas.

Suborder ***Division*** *Family*	*British Fauna*[a]	*World Fauna*[b]
Nematocera		
Cecidomyiidae*	0/630	6/4500
Brachycera		
Acroceridae	3	475
Bombylidae	10	3000
Nemestrinidae	0	300
Cyclorrhapha		
Acalypterae		
Phoridae*	0/250	300/3000
Pipunculidae	75	600
Conopidae	24	800
Calypterae		
Sarcophagidae*	53	1250/2500
Tachinidae	234	8200

* Family contains many species that are not true parasitoids. Where one figure is given, it refers to the size of the whole family; where two figures are given, e.g., 10/20, 10 species out of 20 are parasitoids. In Phoridae and Sarcophagidae, the figure for the total number of parasitoid species is obtained by extrapolation from the proportions with known biology.

[a] Data from K.G.V. Smith 1976.

[b] Data from Eggleton and Belshaw 1992, and Belshaw, pers. comm.

Table 1.3
Families of parasitoids, other than those in the Hymenoptera and Diptera, mentioned in the text, and the number of described species in the British and world faunas.

Order *Family*	*British Fauna*[a]	*World Fauna*[b]
Coleoptera		
Carabidae*	362	470/30000
Staphylinidae*	990	500/30000
Rhipiphoridae	1	400
Meloidae*	9	2000/3000
Stylopoidea (=Strepsiptera)[c]*	15	10/400[d]
Lepidoptera		
Pyralidae	0/208	1/20000
Epipyropidae	0	10/20
Neuroptera		
Mantispidae	0	50/250

* Family contains many species that are not true parasitoids. Where one figure is given, this refers to the size of the whole family, where two figures are given, e.g., 10/20, 10 species out of 20 are parasitoids.

[a] Data for Coleoptera from Pope 1977.

[b] Data from Eggleton and Belshaw 1992, and Belshaw, pers. comm.

[c] The Stylopoidea is a superfamily.

[d] The biology of the Stylopoidea is difficult to categorize; see text.

the families of dipterous parasitoids mentioned in the text with some information on their numerical importance; figure 1.1 illustrates the adults of two important families. Eggleton and Belshaw (1992) provide a catalog of the distribution of parasitoids among dipteran families.

1.4.3 Coleoptera and Other Orders

A small number of beetle families contain parasitoids (table 1.3). The large families Carabidae (ground beetles) and Staphylinidae (rove beetles) include a few species that are parasitoids of soil arthropods. The Rhipiphoridae and Meloidea contain species that are parasitoids of larval bees and wasps. Eggleton and Belshaw (1992) catalog the occurrence of parasitoids among beetle families.

The superfamily Stylopoidea was until recently accorded ordinal status as the Strepsiptera. One primitive family (the Mengeidae) contains parasitoids of Thysanura (apterygote insects including the silverfish) while other families attack ants, bees, wasps, and hemipterans. This latter group are perhaps best regarded as true parasites: male and female larvae develop in the host hemocoel until the final instar, when they force their heads through an intersegmental membrane and pupate. The adult female remains in situ throughout her adult life and produces a very large number of eggs while the adult male leaves the host and searches for females. Insects that have been attacked by female stylopoids normally do not die, although very frequently they are castrated. Insects attacked by some species of males do die, and in these cases the male stylopoid can be considered a parasitoid. The stylopoid life history is thus in some ways intermediate between parasitoids and parasites. Further details of their biology can be found in Askew (1971) and Waloff and Jervis (1987).

There are a very few species of parasitoid among the moths (Lepidoptera) and the lacewings (Neuroptera) (Askew 1971). Very recently, a caddisfly (Trichoptera) has been found to develop as a parasitoid of other caddisflies (Wells 1992).

1.5 Evolutionary Transitions

In this section I briefly discuss ideas about the evolution of the parasitoid habit and the biology of species that have evolved from parasitoids. This subject has been recently reviewed by Eggleton and Belshaw (1992) in a careful cladistic analysis of the available evidence.

1.5.1 The Evolution of the Parasitoid Habit

The parasitoid habit has probably evolved just once within the order Hymenoptera, although many times in the Diptera and Coleoptera. Within the Hymenoptera, the Apocrita plus the single symphytan family Orussidae form a holophyletic assemblage containing all the parasitoids and groups that evolved from parasitoids. Where the biology is known, the Orussidae are parasitoids of insects living in dead wood, including other sawflies. Some idea of how the parasitoid habit may have evolved can be obtained by examining the biology of what is possibly the sister group to the Aprocrita+Orussidae clade, the sawfly superfamily Siricoidea (*sensu lato*). The sawflies of the Siricoidea (the best known species is probably the Wood Wasp *Urocerus gigas*) generally feed on dead wood that has been digested by symbiotic fungi. Some siricoids lack symbiotic fungi and make use of fungi associated with other species. A plausible hypothesis for the evolution of the parasitoid habit is that a species of siricoid which did not possess a fungus evolved to kill other species which did, and then progressed from only killing the donor to eating it as well (Eggleton and Belshaw 1992; see Malyshev (1968) for a related idea based upon a different phylogenetic hypothesis). If this hypothesis is correct, the parasitoid habit evolved from mycophagy in the Hymenoptera. Several groups of coleopterous parasitoids have evolved from mycophagous ancestors in dead wood (for example, the Rhipiphoridae). Crowson (1981) has proposed an essentially similar hypothesis to explain the evolution of the parasitoid habit in these groups.

Another important evolutionary pathway to the parasitoid habit is through feeding on dead and decaying insects (saprophagy). The dipteran family Sarcophagidae contains many species that feed on dead and decaying insect larvae and some species have evolved into true parasitoids that attack and cause the death of their hosts. The Sarcophagidae are closely related to the large and important family of dipteran parasitoids, the Tachinidae, and it is likely that they also evolved from saprophages.

The two beetle families Staphylinidae and Carabidae are almost exclusively predatory in habit but contain a few small-sized species that have become parasitoids. The transition from a predator to a parasitoid is particularly straightforward since a predator that requires only a single prey item as a larva is by definition a parasitoid. Presumably, the parasitoid habit might evolve by a reduction in the size of the predator, or by an increase in the size of the prey. Eggleton and Belshaw (1992) suggest that a number of dipteran parasitoid groups also evolved from predators.

1.5.2 Life Histories Derived from Parasitoids

The parasitoid habit has been secondarily lost in a variety of different groups. In some cases a single species or genus has adopted a variant life history, but there are a number of examples of major nonparasitoid lineages whose origins can be traced to a parasitoid ancestor.

PROVISIONING PREDATORS

The indistinct boundary between parasitoids and insects that paralyze and move a host to a concealed site prior to oviposition was noted at the beginning of this chapter. In some families of wasps such as the Bethylidae, both types of life history are common. Movement to a concealed site probably evolved as a means to reduce predation, superparasitism, or hyperparasitism of the developing young. A significant consequence of movement is that it allows the parent to add further prey items to the first and so create a cache of food; insects with this life history are termed "provisioning predators." Within the aculeate Hymenoptera, provisioning predation has evolved a number of times from the parasitoid habit and has, in its turn, given rise to groups with other life histories. For example, many bees (Apidae) feed solely on pollen or nectar, while ants (Formicidae) are frequently omnivorous but may also be highly specialized mycophages or seed eaters. Another consequence of the movement of hosts to a concealed site is the evolution of nest-making behavior, an activity that achieves enormous sophistication in the social Hymenoptera.

PREDATION

A number of otherwise typical parasitoids attack more than one host and so must be classed as predators. For example, Taylor (1937) studied the parasitoid community associated with beetles of the genus *Promecotheca*, leaf miners in palms such as coconut and oil palm. Several chalcidoid species such as the eulophid *Hispinocharis (=Achrysocharella) orientalis* and a eupelmid *Eupelmus* sp. were chiefly reared as hyperparasitoids of other parasitoids attacking the beetle. However, a single host was frequently insufficient to complete development, and Taylor observed larvae of both species marauding through the mine consuming any chalcid larva they chanced upon. Similar examples occur among eurytomid, pteromalid, and eulophid parasitoids of gregarious gall formers (Gauld and Bolton 1988). Another eulophid, *Aprostocetus (=Tetrastichus) mandanis*, begins life as a typical egg parasitoid of delphacid homopterans (planthoppers) but then emerges from the egg and searches for other eggs as a predator (Rothschild 1966); several eurytomids have a similar life history (Clausen 1940a). Some phygadeuontine ichneumonids attack a number of social bee larvae in adjacent cells (Daly 1983).

A number of wasps have evolved to oviposit into the egg masses of their hosts; each larva feeds on many host eggs and is thus an egg predator. For example, wasps in the family Evaniidae feed in the egg capsules (oothecae) of cockroaches while the Podagrioninae, a subfamily of the Torymidae, are specialist predators in mantid oothecae. Spider egg masses are also attacked by a number of ichneumonid wasps (Austin 1984, 1985; Fitton et al. 1987).

PHYTOPHAGY (NON-GALL FORMERS)

Several lineages derived from parasitoids have become phytophagous. Most species have close relatives that are parasitoids of insects feeding internally in plant tissue, and it appears that these species have switched from feeding on the host to feeding on the host's food. Possibly, phytophagy evolved originally as a means of supplementing the food resources provided by the host. Phytophagy is particularly common in the chalcidoid family Eurytomidae. Wasps in the genus *Tetramesa* mine grass and cereal stems, and those in the genera *Systole* and *Bruchophagus* (possibly a subgenus of *Eurytoma*) feed on the seeds of Umbelliferae and Leguminosae respectively (Claridge 1959, 1961). Some eurytomids begin their larval development as parasitoids but consume plant tissue as they grow older (Varley 1937). A few species of *Gasteruption* (Gasteruptiidae) and *Grotea* (Ichneumonidae) parasitize social insects, eating an egg or larvae, but obtaining most of their nourishment from stored pollen and nectar (Gauld and Bolton 1988).

PHYTOPHAGY (GALL FORMERS)

A number of groups of gall-forming insects are derived from parasitoids. A few *Tetramesa* species (see last paragraph) form modest galls, while extremely complex galls are found in the Cynipidae. The latter family is exclusively phytophagous with most species forming galls although a sizable minority live as inquilines within the galls of other species. Cynipidae are associated with many plant families, with a majority of species forming galls on oaks (Fagaceae). Many species show alternation of generations: a sexual generation followed by an asexual generation. Galls produced by the two generations are frequently different in morphology and may be produced on different plant tissues or even different plant species. Gall morphology can be extremely elaborate but is very consistent, and there has been some debate about how the insect causes the plant to produce such structures. One interesting hypothesis is that the insect injects DNA or RNA into the plant which is incorporated and expressed in the plant genome (Cornell 1983). This idea has yet to be confirmed but, if true, it will be interesting to see if there is any homology between the DNA injected into the plant by cynipids and the DNA injected by parasitoids (as polydnavirus, see sec. 6.3.2) to counteract host defences.

Finally, the natural history of pollinating fig wasps has already been discussed in this chapter (sec. 1.3.3). These wasps provide another example of the transition from the parasitoid habit to gall-forming phytophagy.

PARASITISM

There are a very few example of parasitoids of adult insects that allow their hosts to reproduce before killing them (Askew 1971). Strictly, such species should be called parasites rather than parasitoids. Some scale insects, mealy bugs, and aphids can survive long enough to reproduce after parasitism. A number of euphorine braconids (e.g., *Perilitus*) oviposit into adult beetles and may emerge without killing their host (Shaw and Huddleston 1991). The host continues to feed and reproduce and, exceptionally, acts as a host for a second generation of wasp (Timberlake 1916). Adult Hemipterans also sometimes recover from attack by tachinid flies (Worthley 1924). Recovery from parasitism by larval insects is much rarer; the examples I know all concern lepidopteran caterpillars attacked by tachinid flies (Richards and Waloff 1948; DeVries 1984; and English-Loeb et al. 1990). In the last case, English-Loeb et al. (1990) found that about 25% of caterpillars of the arctiid moth *Platyprepia virginalis* that were attacked by the gregarious tachinid *Thelairia bryanti* survived their ordeal. Although they took longer to develop, their fecundity as adults was not impaired.

The curious biology of the Stylopoidea has already been discussed in this chapter, where it was suggested they are best regarded as parasites. The most primitive members of the superfamily as parasitoids and it is possible that all members of the group are derived from parasitoid ancestors.

1.6 Conclusions

Parasitoids are abundant components of nearly all terrestrial ecosystems, both in terms of numbers of species and numbers of individuals. Although some unusual variants exist, the majority of parasitoids have broadly similar life histories and face many similar evolutionary challenges, which are explored in subsequent chapters. Parasitoids must locate hosts in a complicated and heterogeneous environment (chapter 2) and on finding a host make a series of reproductive decisions. The parasitoid must decide whether the host is suitable for oviposition and, in the case of gregarious species, decide how many eggs to lay (chapter 3). Hymenopterous parasitoids, whose females have proximate control of the sex ratio, must also decide whether to produce male or female eggs (chapter 4). The study of sex allocation in parasitoid wasps is complicated by the recent discovery of a variety of non-Mendelian factors that can influence observed sex ratios (chapter 5). The fate of the developing parasitoid is strongly influenced by host quality and, in the case of koinobiont species, by defenses against parasitism mounted by the host. Parasitoids, in their turn, have evolved counteradaptations to host defenses (chapter 6). The size and fitness of the adult parasitoids is also influenced by the quality of the host in which it developed. The adult parasitoid faces many of the same challenges as other insects, such as finding a mate and avoiding predation (chapter 7). Finally, host ecology and the presence of competing species of parasitoid combine together with phylogenetic considerations to determine the overall life history of the parasitoid: for example, the division of resources between reproductive and trophic functions, and the balance between egg size and number (chapter 8).

I hope to show in this book that parasitoids are not only fascinating organisms for study in their own right, but that their often unique biology allows valuable insights into many aspects of natural selection and adaptation.

2

Host Location

Considering the small size of both parasitoids and their hosts, and also the structural complexity of the environments inhabited by most parasitoids, finding a suitable host appears a formidable task. This chapter is concerned with the behavioral ecology of host location in parasitoids.

Research into host location by parasitoids falls into two main schools. One school has concentrated on trying to understand the behavioral mechanisms used by the parasitoid to locate their hosts. This research program, started in the 1930s, has been spectacularly successful in revealing the complex assemblages of cues used by parasitoids in host location. A major motivation behind this research has been the prospect of manipulating the stimuli perceived by the parasitoid to enhance biological control. Recent research in this field has emphasized the plasticity of response by parasitoids to different cues, and the importance of learning. The origins of the second school are more recent and lie in the explosion of interest in behavioral ecology in the 1970s. A cornerstone of the new field is optimal foraging theory, which seeks to predict the feeding behavior of animals on the assumption that behavior is optimized by natural selection. Searching for hosts has much in common with foraging for food, and the classical models of foraging theory were soon applied both to host location and host acceptance (chapter 3).

In the first section of this chapter I discuss a number of broad conceptual models that have been employed to organize discussion of host location in parasitoids. The second section is a brief review of the amazing variety of host location mechanisms that have been discovered in parasitoids, while the third section describes the evidence for plastic responses and learning. Comparative studies of host location in parasitoids are still in their infancy, but the fourth section describes pioneering work on a guild of parasitoids of Diptera. In the final section I discuss how parasitoids respond to the spatial distribution of their hosts and, in particular, the application of ideas from foraging theory to parasitoid searching.

2.1 Conceptual Models of Host Location

Host location and attack is traditionally discussed using a conceptual model first developed by Salt (1935) and Laing (1937). Salt divided host location and attack into “ecological” and “psychological” components, the former incorporating habitat and to a certain extent host location, while the latter referred chiefly to host acceptance. Successful parasitism also required host suitability. Laing developed this theme by arguing that host finding was a two-stage process involving host habitat location followed by host location.

The division of successful parasitism into the hierarchical process of host habitat location, host location, host acceptance, and host suitability has been immensely influential and has been adopted by nearly all authors reviewing the subject (Flanders 1953; Doutt 1959, 1964; Vinson 1976, 1984, 1985; Vinson and Iwantsch 1980a; Nordlund et al. 1981; van Alphen and Vet 1986; Wellings 1991). Some authors have inserted further divisions, for example dividing host acceptance into examination, probing, drilling, and oviposition (Vinson 1985). Although there has been general recognition that these "divisions are primarily for our convenience in thought and communication" (Vinson 1981), this conceptual model has tended to emphasize a static hierarchical view of parasitoid behavior.

A much more dynamic model has been proposed recently by Lewis et al. (1990) and Vet et al. (1990). They first point out that stimuli will vary in their information content and that the parasitoid should respond to the stimulus most closely associated with the host. Thus host habitat location is redundant if the parasitoid is able to locate the host directly. They envisage a naive parasitoid being born with an innate set of "response potentials" to different stimuli; a parasitoid presented with a number of stimuli will react to the one with the highest response potential (fig. 2.1). The ranking of different stimuli will be fine-tuned by natural selection to maximize the parasitoid's chance of successful host location.

Lewis, Vet, and colleagues stress that the ranking of different stimuli will change over the life of the parasitoid. In particular, if a parasitoid finds that a certain stimulus is associated with the presence of hosts, its ranking may increase. Thus a naive parasitoid might initially locate a host using a chemical stimulus emitted by the host or even by chance. After finding a host on a particular food plant, it might then use volatile chemicals associated with that food plant in future host location: a latent response to the food plant is promoted through experience (fig. 2.1). Within a species, not all individuals will rank stimuli in the same way. Genetic differences will arise due to local adaptation, and Lewis et al. speculate that there may be within-population genetic differences as well. Finally, response potentials will be modified by physiological state; a hungry individual may not respond to stimuli associated with host location, but prefer to forage for food instead.

This model is an advance on the strictly hierarchical view of host location. However, in stressing the behavioral responses to chemical stimuli, the model leaves little room for other strategies that explicitly involve movement in space, such as systematic search. It thus may also be useful to think of host location by parasitoids in terms of the model illustrated in figure 2.2. Superimposed on the real world is a surface, the height of which represents the parasitoid's esti-

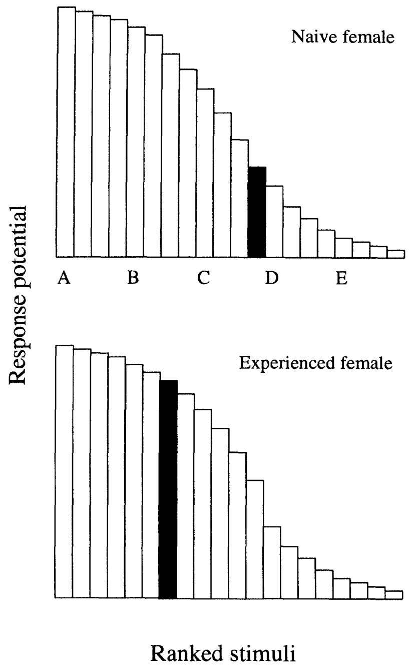

Figure 2.1 Lewis, Vet, and colleagues assume that a naive female wasp has an innate tendency to respond to an array of different stimuli (a response potential). They speculate that the distribution of response potentials is sigmoid, although this is not essential for their argument. The stimuli most closely associated with the host will have the highest response potential; thus *A* may be a volatile chemical produced by the host, *B* a chemical associated with the frass, and so on down to the lowest-ranking stimuli, which might be associated simply with the host habitat. Suppose that the filled bar in the top figure is the response potential associated with a potential food plant of the host. If a female finds hosts on this particular plant species, the response potential to the host plant stimulus may increase (bottom figure, filled bar).

mation of the presence of a host (in reality three-dimensional, though shown for simplicity in one dimension). The parasitoid will be selected to move toward a host; it will do this most efficiently by climbing the steepest slope of the likelihood surface. Directional stimuli with different information values represent different slopes of this surface. Of course, the parasitoid's estimation of the likelihood of discovering a host may be flawed, and one can imagine a parallel surface representing the true likelihood of host discovery. However, natural selection will act to make the two surfaces as congruent as possible.

The pictorial model can also be used to illustrate the parasitoid's actions on entering a region where the probability of locating a host is high but where there are no directional stimuli: the insect is now on the edge of a plateau, the plateau containing a further, invisible peak. The parasitoid should now search the plateau systematically, turning back on encountering the edge of the pla-

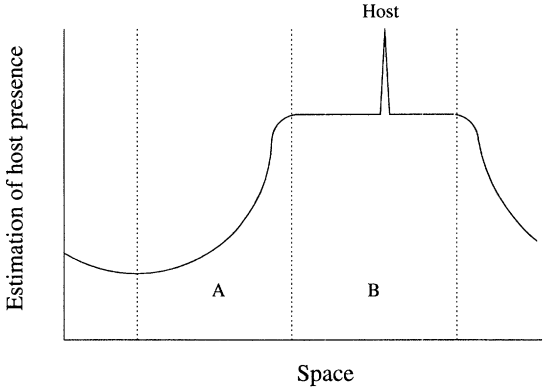

Figure 2.2 The relationship between directional search and patch use. The parasitoid's estimation of the presence of a host is plotted in a one-dimensional space. The insect will be selected to make use of stimuli that carry directional information; an individual in region *A* will thus move to the right, perhaps up the concentration gradient of a volatile chemical associated with the host. When it is in region *B*, the parasitoid obtains no directional information and makes use of other searching strategies to locate the host. The insect will, however, often turn back at the edge of the "plateau." As discussed in the text, the shape of the estimation surface may be influenced by previous experience and the presence of other searching parasitoids.

teau, and reacting to any further increase in height that may indicate the precise location of the host.

After the parasitoid has located and parasitized a host, the contours of the likelihood surface change in a manner that reflects the spatial distribution of the host. If the host tends to be solitary, what was a peak becomes either a hole or a point on a plain, and the parasitoid moves off in search of further hosts. If the host tends to be gregarious, the height of the plateau may be reduced but the insect may still remain in the area, attracted to a nearby peak, or systematically searching the plateau in the hope of further host encounters. The shape of the likelihood surface will also be influenced by past experience; as Lewis et al. (1990) and Vet et al. (1990) stress, a stimulus may offer much greater information about the location of a host if the parasitoid has already encountered a host associated with the source of the stimulus. Finally, the decisions made by the parasitoid may be affected not only by the spatial distribution of the host, but also by the distribution of searching competitors.

2.2 Mechanisms of Host Location

Parasitoid biologists have made enormous advances in recent years in understanding the cues and stimuli used by parasitoids to locate hosts (important reviews: Vinson 1976, 1981, 1984, 1985; Waage 1978; R. L. Jones 1981;

Weseloh 1981; Nordlund et al. 1988; Vet and Dicke 1992). Here, no attempt will be made to provide a comprehensive review of this field, though a range of examples of the mechanisms involved in host location will be described. The intense selection pressure that parasitoids experience in locating hosts is well illustrated by the variety of subtle cues used in host searching. I will distinguish three broad categories of information that are used in host location: stimuli from the host microhabitat or foodplant, stimuli indirectly associated with the presence of the host, and stimuli arising from the host itself. Although the categories blend into each other, the ranking roughly reflects increasing importance as indicators of host presence.

Another important distinction, particularly appropriate to chemical cues, is whether or not the stimulus imparts directional information. Dethier et al. (1960; see also Waage 1978) distinguished between *attractant chemicals* that insects use to locate hosts, and *arrestant chemicals* which, while not providing directional information, reveal the possible presence of the host in the near vicinity. In terms of the metaphor of figure 2.2, attractants determine the slope of the host likelihood surface while arrestants define the boundaries of the plateaus. Arrestant chemicals tend to have higher molecular weight and lower volatility in comparison with attractant chemicals. The study of chemical arrestants has been an extremely active area of research because of their possible economic significance: it has been suggested that the application of these chemicals to crops may result in parasitoids remaining longer in the vicinity of the crop, thus destroying more pests (Gross 1981).

Chemicals that convey information between two species are sometimes called *allelochemicals.* If both the receiver and signaler benefit from the exchange of information, the allelochemical is called a *synomone*; if the receiver alone benefits, the chemical is called a *kairomone*; and if the signaler alone benefits, an *allomone.* Chemicals that convey information between the members of one species are called *pheromones.* Allelochemicals and pheromones are the two classes of *infochemical* (Nordlund and Lewis 1976; Dicke and Sabelis 1988; Vet and Dicke 1992).

In this section, I first describe examples of host location by parasitoids using cues associated with the host habitat, indirectly with the host, and with the host itself. I also discuss host location by phoresy—hitching a ride on the adult host. The final part of this section describes host location in parasitoids which oviposit away from the host and which require either the ingestion of the parasitoid egg or active search by the parasitoid larva.

2.2.1 Cues from the Microhabitat and Host Plant

It is well established that chemical cues from the host's microhabitat can attract parasitoids in the absence of the host itself. As long ago as 1937, Laing demonstrated that the braconid *Alysia manducator* and the pteromalid *Nasonia (=Mormoniella) vitripennis*, both parasitoids of carrion flies (*Calliphora*), were attracted to uninfested meat. In the same year, Thorpe and Jones (1937) showed that the ichneumonid *Venturia (=Nemeritis) canescens*, which attacks stored product moths, was attracted to clean oatmeal.

More recently, Vet, van Alphen and their coworkers have conducted extensive investigations on microhabitat location in various parasitoids of Drosophilidae. Drosophilid parasitoids, chiefly braconids and eucoilids, tend to specialize on flies living in different microhabitats such as fungi, decaying leaves, fruit, and sap exuding from trees. Vet (1983, 1985a), Vet et al. (1983, 1984a), and van Alphen et al. (1991) found that most microhabitat specialists were attracted to odors produced in that microhabitat, often by yeasts (Dicke et al. 1984). In some cases, a more fine-tuned location mechanism was found. Thus the eucoilid *Leptopilina clavipes* is only attracted to mature fungi, just beginning to decay, the stage at which it is attacked by the wasp's host (Vet 1983). In another case, individuals of one species, the braconid *Asobara tabida*, appeared to be either attracted to fruit or to decaying leaves. Further investigation revealed that *A. tabida* was in fact composed of two closely related sibling species, each specialised on its own microhabitat (Vet *et al.* 1984a).

The importance of the host plant for parasitoid searching is suggested by several lines of indirect evidence. Taxonomically unrelated hosts feeding on the same species of plant frequently share the same parasitoids, indicating that host location is influenced by the host plant (Picard and Rabaud 1914). Similarly, the amount of parasitism suffered by a polyphagous host species often depends on the food plant it attacks (Vinson 1981, 1985; Nordlund et al. 1988).

Stronger evidence for the importance of host plant odors has been obtained from behavioral studies in the laboratory, first using Y-tube olfactometers, but more recently from multiple-choice olfactometer (Vet et al. 1983) and wind tunnel experiments (e.g., Elzen et al. 1986; Drost et al. 1986). Thorpe and Caudle (1938) observed that the ichneumonid *Coccophagus turionellae* (= *Pimpla examinator*) was attracted to the odor of pine trees, the food plant of its host, the pine shoot moth *Rhyacionia buoliana*. Curiously, after emergence the wasp takes three or four weeks to mature its eggs and during this period it is repelled by the smell of pine. Arthur (1962) found that the ichneumonid *Itoplectis conquisitor* which also attacks *Rhyacionia buoliana* is attracted to the odor of Scots pine (*Pinus sylvestris*) to a far greater degree than to red pine (*Pinus resinosa*), a preference reflected in the distribution of parasitism in the field.

Read et al. (1970) studied host location by the braconid wasp *Diaeretiella rapae*, which attacks a variety of aphid species, especially those on crucifers. Using olfactometer experiments, they demonstrated that the wasp was attracted to volatile mustard oils released by the host plant. Although the wasp could develop on many aphid species, its response to crucifer volatiles resulted in a restricted host range in nature. Aphids feeding on sugar beet were more frequently parasitized if cabbage (collards) were growing nearby because parasitoids were attracted by the crucifer. In a series of studies, Elzen et al. (1983, 1984a, 1984b, 1986, 1987 and H. J. Williams et al. (1988) have dissected the behavioral response of the ichneumonid *Campoletis sonorensis* to volatile terpenoids produced by cotton, the food plant of its host, larvae of the moth *Heliothis virescens*. The relative attractiveness of different cotton cultivars depends on their production of these volatiles, which are associated with glands on the leaf of the plant. Odors emanating from plants need not always assist the parasitoid in host location. Monteith (1960) suggested that the low rates of parasitism of the larch sawfly (*Pristiphora erichsonii*) by the tachinids *Bessa harveyi* and *Drino bohemica* found in mixed forests as compared with pure stands of larch occur because the odor of the host plant is masked by the volatiles of many different plant species.

Visual and tactile microhabitat cues are also important in host location. Van Alphen (quoted in van Alphen and Vet 1986) observed that the ichneumonid *Diaparsis truncatis* was attracted to wooden models of asparagus berries, the feeding site of its host. Similarly, the braconid *Opius (=Diachasma) alloeum* is attracted to hawthorn berries where its host feeds (Glas and Vet 1983). Visual cues are also used by parasitoids in the final stages of approach and landing after they have been attracted to the host plant by large-range stimuli such as volatile chemicals (McAuslane et al. 1990a; Wäckers and Lewis 1992).

2.2.2 Indirect Cues from the Host

Parasitoids frequently orientate toward cues that are derived from the activity of the host though not actually from the host itself. Again, the majority of these stimuli are chemical in nature.

A number of parasitoids respond to odors released by the feeding activity of their hosts. Damaged pine trees release the terpene α-pinene which attracts the pteromalid wasp *Heydenia unica*, a parasitoid of the bark beetle *Dendroctonus frontalis* (Camors and Payne 1972). Bragg (1974) discovered that the ichneumonid *Phaeogenes cynarae* was attracted to damaged thistles and globe artichokes. When the plant was damaged, either accidentally or by the host, a plume moth (*Platyptilia carduidactyla*), parasitoids could be observed flying upwind to inspect the damaged tissue. The braconid *Cotesia (=Apanteles) rubecula* is also attracted to plants damaged by its host (the butterfly *Pieris rapae*), but in this case artificial damage fails to elicit the same response (Nealis 1986).

Recent studies are beginning to reveal the complexity of the tritrophic interaction between host plant, host, and parasitoid. Attack by the cassava mealy bug (*Phenacoccus manihoti*) causes extensive changes to the physiology of the host plant. The encyrtid, *Epidinocarsis lopezi*, is attracted to damaged cassava though not to either cassava alone or the mealy bug alone. Uninfested leaves from infested plants are also attractive (Nadel and van Alphen 1987). The braconid parasitoid *Cotesia (=Apanteles) marginiventris* reacts to a variety of stimuli emanating from the host and host plant. Turlings et al. (1991a) found that the weakest response was to host larvae, the next strongest was to host frass, but by far the most important response was to damaged leaves. The wasp responds much more strongly to leaves that have been damaged by the host than to artificially damaged leaves (Turlings et al. 1990b). However, if saliva from the host caterpillar (the fall army worm, *Spodoptera exigua*) is placed on artificially damaged leaves, the wasp responds as if to host feeding. It appears that a chemical in the caterpillar's saliva causes the plant to release heavy terpenoids and indole, which are attractive to the parasitoid (Turlings et al. 1990b, 1991a, 1991b). The chemicals are released not only from the site of attack, but systemicly by the rest of the plant (Turlings and Tumlinson 1992). Many of the responses of the parasitoid to host and plant-derived stimuli increase dramatically with experience (see sec. 2.3). These studies raise the intriguing possibility that the plant may be selected to produce volatile chemicals that attract natural enemies of its herbivores (see sec. 8.2.5).

Even when the host does not actively damage the plant, there may be interactions between odor cues derived from the host and the host plant. For example, Kaiser et al. (1989) found that naive females of the egg parasitoid *Trichogramma maidis* (Trichogrammatidae) did not respond to odor from host eggs (the European corn borer, *Ostrinia nubilalis*), to host sex pheromone or to an extract from the host plant (maize). However, they did respond to a combination of the three odors. These examples emphasize the artificiality of separating host habitat location from host location.

Volatiles released by other organisms, as well as by the host, may be used in host location; their usefulness naturally depends on the closeness of their association with the host. The braconid *Diachasmimorpha (=Biosteres) longicaudatus*, which attacks tephritid fruit flies, is attracted to acetaldehyde, ethanol, and acetic acid released by a fungus that grows on peaches (Greany et al. 1977). Many of the volatile chemicals used by *Drosophila* parasitoids in host location are produced by yeasts in the substrate (Dicke 1988). A much stronger association is that between the parasitoids of wood wasps (*Urocerus (=Sirex)* spp.) and their symbiotic fungus (*Amylostereum* sp.). The larvae of the wood wasp bore into timber but can feed only on wood attacked by the fungus; the parent wasp inoculates the tree with the fungus at oviposition. A range of ichneumonids in the genera *Rhyssa* and *Megarhyssa* and of ibaliids in the genus *Ibalia* are all attracted to volatile chemicals produced by the fungus (Madden 1968; Spradbery 1970a, 1970b). This story is further complicated by the activities of another ichneumonid, the cleptoparasitoid *Pseudorhyssa sternata*. This species is unable to drill its own oviposition shaft and can only oviposit using the shafts made by *Rhyssa*. Like *Rhyssa*, it is attracted to wood infested by the host fungi though, in addition, it responds to a glandular secretion of *Rhyssa* which it uses to locate the oviposition shaft (Spradbery 1969). A similar example is provided by the ichneumonid *Temelucha interruptor* which uses the odor of the braconid *Orgilus obscurator*, to locate its host, the pine shoot moth *Rhyacionia buoliana* (Arthur et al. 1964)—the ichneumonid tends to win in competition with the braconid. *Ichneumon eumerus* (Ichneumonidae) parasitizes the caterpillars of blue butterflies (*Maculinea rebeli*) which feed inside ant nests (Thomas and Elmes 1993). The wasp detects the entrance of nests using chemical cues from the ants and is able to distinguish ant nests of the correct species (*Myrmica schencki*) from those of several congeners in the same habitat. Wasps approach all nests of the right species but only enter nests containing caterpillars. How they detect the presence of the butterfly at close range is not known. Chemical cues may be involved although auditory cues are also a possibility; *Maculinea* caterpillars produce sounds that are similar to, though clearly distinguishable from, ant workers.

The activity of the adult host at oviposition is the source of a number of arrestant chemicals. One of the best studied short-range chemical stimuli is a substance, tricosane, found on the scales of moths that are dislodged during oviposition. Trichogrammatid egg parasitoids (*Trichogramma* spp.) are less likely to disperse from an area after detecting the arrestant stimulus (Laing 1937; Lewis et al. 1971a, 1972, 1975a, 1975b; R. L. Jones et al. 1973; Nordlund et al. 1977). Although the scales help parasitoids to locate hosts, they probably also protect the egg batch from predators. The braconid *Opius lectus* is able to detect an oviposition site marker deposited by its host, the tephritid fruit fly *Rhagoletis pomonella* (Prokopy and Webster 1978). The marker is placed by the fly to deter conspecific oviposition. Similarly, the pteromalid *Halticoptera rosae* detects a site marker deposited by *Rhagoletis basiola* (Roitberg and LaLonde 1991). Female *R. basiola* that do not mark their oviposition sites are found at low frequencies in the field, and Roitberg and LaLonde suggest parasitoid attack may lead to a polymorphism in the host population (see sec. 3.3.3).

Some parasitoids use stimuli produced by host adults to help in the location of the immature stage which they attack. The usefulness of such stimuli obviously depends on the closeness of the association between adult and juvenile. There is a close association in bark beetles (Scolytidae); the adults inhabit the same galleries in the bark as the larvae. Bark beetles emit an aggregation pheromone which in a number of cases has been synthesized and used in pest management. Kennedy (1979) discovered that one such preparation, "multilure," attracted a variety of pteromalid, eulophid, and braconid parasitoids of bark beetle larvae (*Scolytus multistriatus*). In addition, a pteromalid hyperparasitoid of the beetle also responded to the pheromone. The braconid parasitoid *Aphidius ervi* uses aphid alarm pheromone in host location (F. Pennacchio, quoted by Vinson 1990a). The juvenile stage most closely associated with the adult insect is the egg, and some egg parasitoids use adult sex pheromone in host location. Lewis et al. (1982) found that egg parasitoids (*Trichogramma* sp.) responded to the sex pheromone of their host, the moth *Heliothis virescens* (see also Noldus and van Lenteren 1985; Noldus 1989). The sex pheromone is adsorped and retained on the surface of the leaf and thus provides information about the past presence of a sexually active adult (Noldus et al. 1991). Three species of braconid wasp in the genus *Praon* were attracted to the synthetic sex pheromone of their aphid host (Hardie et al. 1991). Read et al. (1970) discovered that males of the braconid parasitoid of aphids, *Diaeretiella rapae*, were attracted to a volatile chemical produced by female wasps, and this chemical also attracted the cynipid *Alloxysta (Charips) brassicae*, a hyperparasitoid attacking *D. rapae* larvae. The hyperparasitoid showed no attraction to plants or aphids and thus only orientated toward parasitized aphid colonies.

Other important sources of arrestant or short-range attractant chemicals include frass and honeydew. For example, the braconid *Microplitis croceipes*, a parasitoid of the corn earworm (*Helicoverpa zea*), responds by antennation to 13-methylhentriacontane, a chemical in the host frass (Lewis 1970; Lewis and Jones 1971; R. L. Jones et al. 1971). Many homopterans produce large quantities of honeydew which both reveal their presence and provide food for parasitoids. The encyrtid *Microterys nietneri (=flavus)* responds to fructose and sucrose as well as to some other unidentified compounds in the honeydew secreted by its host *Coccus hesperidum*, the brown soft scale (Vinson et al. 1978). Aphid parasitoids frequently respond to honeydew (Bouchard and Cloutier 1984, 1985; Ayal 1987). The braconid *Diaeretiella rapae* searches crucifers for its host, the cabbage aphid *Brevicoryne brassicae*. It flies first to the base of the crucifer and only if it discovers honeydew, which tends to drip or get washed to the base, does it embark on a more careful search of the plant (Ayal 1987). Some scale insect parasitoids respond to chemicals present in the wax of their host (Takabayashi and Takahashi 1985).

Mandibular and labial gland secretions, chiefly of lepidopterous hosts, are an important source of short-range attractants and arrestants. Stored product moths (Pyralidae, Phycitinae) secrete chemicals from their mandibular gland that may act as a dispersal pheromone (Corbet 1971). The well-studied ichneumonid *Venturia canescens* uses these substances (2-acylcyclohexane-1,3-diones) as an arrestant stimulus (Mayer 1934; Thorpe and Jones 1937; Corbet 1971, 1973; Mudd and Corbet 1973, 1982; Mudd et al. 1984; Waage 1978). The braconid *Bracon hebetor*, which attacks the same host, also uses the mandibular secretions for the same purpose (Strand et al. 1989). *B. hebetor*, but not *V. canescens*, will follow trails made by the host containing traces of the kairomone. The reason for this difference in behavior is that *B. hebetor* attacks mature larvae and *V. canescens* young larvae, and that older larvae enter a wandering phase prior to pupation. Another very well studied behavior is the arrestant response of the braconid *Cardiochiles nigriceps* to mandibular secretions of its hosts, moths in the genus *Heliothis* (Vinson and Lewis 1965; Vinson 1968; Vinson et al. 1975). Substances associated with silk produced by the labial gland are also known to act as short-range cues; a good example of this is provided by the braconid parasitoid *Cotesia (=Apanteles) melanoscelus*, a parasitoid of the gypsy moth (*Lymantria dispar*) (Weseloh 1976a, 1977, 1981).

There are some examples of indirect visual cues that are used in host location. Arthur (1966) found that the ichneumonid *Itoplectis conquisitor* was attracted to leaf rolls made by its host, the moth *Rhyacionia buoliana.* Leaf-mining insects leave a visual trace of their feeding activities which is often visible from some distance. A number of their parasitoids are known to respond to this visual cue by alighting preferentially on mined leaves (Kato 1984; Sugimoto et al. 1986, 1988b, 1988c; Casas 1989).

Some hosts leave "trails" over their environment which can be followed by parasitoids to their source (Klomp 1981). For example, many leaf-mining insects produce sinuous linear mines. The braconid *Dapsilarthra rufiventris* and the eulophid *Chrysocharis pentheus (=Kratochviliana* sp.), which attack an agromyzid fly (*Phytomyza ranunculi*) in buttercup leaves (*Ranunculus glaber*), move over the surface of the leaf until a mine is discovered, which is then followed until a host is encountered. If the mine begins to narrow, the parasitoids realize they are going the wrong way (i.e., toward the egg instead of towards the host) and reverse direction (Sugimoto 1977; Sugimoto et al. 1986, 1988a, c). Kato (1984, 1985) has suggested that some insects produce mines that are shaped to confuse parasitoids.

2.2.3 Direct Cues from the Host

A famous anecdote about long-range parasitoid orientation to chemical cues emanating from the host concerns the response of the ichneumonid *Pimpla bicolor* to cocoons of its host, the lymantriid moth *Euproctis terminalia.* "If a cocoon of the moth be broken open in the forest, both pupa and the hands and arms of the observer are covered by a swarm of the parasite females within the matter of a few minutes, although few or no parasites may have been observed in the vicinity previously. The range over which this attraction becomes effective so rapidly must be comparatively extensive to produce this phenomenon. The normal attraction of the pupa within the cocoon is no doubt intensified by breaking open the latter" (Ullyett 1953).

Selection will normally act on hosts to reduce the emission of volatile chemicals if they are used by parasitoids for host location. However, there are cases where hosts deliberately emit volatiles for their own purposes, as sex pheromones or aggregative pheromones for example, and these chemical advertisements are exploited by the parasitoid. The green stink bug (*Nezara viridula*, Pentatomidae) emits a chemical that acts as an aggregative and possibly also a sex pheromone. The tachinid *Trichopoda pennipes* which lays its eggs on the adult insect uses the chemical to locate its host (Mitchell and Mau 1971; Harris and Todd 1980). Clausen (1940a) remarks that many tachinid flies which parasitize the adult stages of a variety of insects are largely reared from the female sex, and it is possible that host location by sex pheromones is responsible. Feeding by bark beetles on trees is facilitated by mass attack, which is accomplished by the emission of an aggregative pheromone. The pteromalid *Tomi-*

cobia tibialis attacks adult bark beetles in the genus *Ips* and is attracted to the aggregative pheromone of its hosts, but not to that of closely related species (Rice 1968, 1969). The response of the parasitoid to host kairomones derived from geographical strains of the same species also varies (Lanier et al. 1972). Sex pheromone produced by the California Red Scale (*Aonidiella aurantii*) serves as an attractant chemical for aphelinid parasitoids (*Aphytis* spp.) (Sternlicht 1973).

Though the detection of chemical cues seems to be the most frequent method of host location, some parasitoids make use of other senses. A few parasitoid flies are known to be attracted by the sound of their host: the tachinid *Euphasiopteryx ochracea* to crickets (Cade 1975, 1981, 1984; Mangold 1978) and the aptly named sarcophagid *Colcondamyia auditrix* to cicadas (Soper et al. 1976). Both species are attracted by tape recordings of their host. Richerson and Borden (1972) suggested that the braconid *Coeloides brunneri* used infrared radiation to detect its host, a bark beetle. They discovered that the wasp would investigate areas of bark heated by as little as 1°C. However, it is possible that convection or conduction rather than radiation were responsible for heat perception (Weseloh 1981).

Substrate vibration is often used by parasitoids, especially those attacking concealed hosts. Oviposition by the braconid *Coeloides brunneri*, a bark beetle parasitoid, can be induced by scratching the undersurface of the bark with a pin (Ryan and Rudinsky 1962; but see Richerson and Borden 1972). Similarly, the braconids *Opius melleus, Diachasmimorpha (=Biosteres) longicaudatus* and *Opius (=Diachasma) alloeum*, all of which parasitize larval tephritid fruit flies, locate hosts through their movement (Lathrop and Newton 1933; Lawrence 1981a; Glas and Vet 1983). Many eucoilid and braconid parasitoids of *Drosophila* use substrate vibration (Vet and van Alphen 1985; Vet and Bakker 1985), as do parasitoids of grain weevils (van den Assem and Kuenen 1958) and leaf-mining flies (Sugimoto et al. 1988a, 1988b).

Movement by the host, detected visually, frequently guides parasitoids in the final stage of host location. The tachinid *Drino bohemica* which attacks sawfly larvae (*Neodiprion lecontei*) detects nearby hosts by their movement (Monteith 1956, 1963). Adult insects tend to be more mobile than larvae and their parasitoids, in particular, use movement to locate hosts; two good examples are the tachinid *Trichopoda pennipes*, which attacks adult stink bugs (*Nezara viridula*) (Mitchell and Mau 1971), and the pteromalid *Tomicobia tibialis*, which attacks adult bark beetles (*Ips* sp.) (Rice 1968). The braconid subfamily Euphorinae contains many species that attack adult beetles, particularly weevils, and host movement is normally important in the final stages of host location (Shaw and Huddleston 1991).

A relatively small number of parasitoids attack swiftly moving adult insects which they intercept in flight. Hosts are detected visually and these parasitoids often have large eyes. Conopids are large robust flies that mostly parasitize bees and wasps. The fly may mimic the flight of its host before pouncing and laying an egg in midflight (Raw 1968). Female *Conops scutellatus* loiter near the entrance of wasp nests and pounce on insects as they exit or enter (Clausen 1940a). A tachinid fly, *Rondanioestrus apivorus*, deposits larvae (from eggs it has incubated in its reproductive tract) on worker bees in flight (Skaife 1921). The aberrant conopid genus *Stylogaster* follows columns of army ants and parasitizes a variety of adult insects that are flushed by the ants (Askew 1971). Pipunculids are flies with very large eyes that parasitize homopteran nymphs (or occasionally adults). Members of this family are famed aerial acrobats and are able to hover and even fly backwards. They locate their hosts visually, swooping down to carry them into the air where parasitism occurs (Clausen 1940a). Another famous example of aerial attack is provided by a phorid fly in the genus *Apocephalus*. It again locates its hosts, workers of leaf-cutter ants (*Atta*), by sight and flies down to lay an egg quickly on the ant's neck. The ant is able to defend itself with its mandibles, except when it is returning to the nest carrying a leaf fragment. However, in these circumstances a minute worker of a separate caste rides shotgun on the leaf and protects the larger worker (Eibl-Eibesfeldt and Eibl-Eibesfeldt 1968).

2.2.4 Phoresy by Adult Parasitoids

The majority of parasitoid hosts are immature insects. One way of locating immatures is to hitch a ride on the adult and wait until it oviposits or returns to a nest. Phoresy has been recorded in a number of parasitoids, and has been reviewed by Clausen (1976) and Vinson (1985).

Egg parasitoids in particular are likely to benefit from phoresy because of the physical contact between the adult and the egg. For example, the scelionid *Mantibaria (=Rielia) mantis* attaches itself to adult mantids (*Mantis religiosa*), where it loses its wings and waits until the mantid oviposits. If it finds itself attached to a male it transfers to the female during mating. There is some evidence that the female wasp may feed from the adult mantid as a true parasite. When the mantid oviposits, the wasp jumps off and parasitizes the egg. The now wingless wasp is not deterred by the frothy liquid used by the mantid to cover her eggs. After parasitism, the wasp attempts to remount the adult mantid (Rabaud 1922; Chopard 1923). The parasitoid is unable to attack host egg masses after the frothy liquid has hardened and the necessity of locating newly laid egg batches is likely to have been important in the evolution of phoresy. The members of the family Scelionidae are all egg parasitoids and a number are phoretic on grasshoppers, moths, planthoppers, and even dragonflies (Clausen 1976). The Trichogrammatidae are also exclusively egg parasitoids and a few phoretic species are known. A species of *Xenufens* attaches itself to the base of butterfly wings (*Caligo eurilochus*). In one population, Malo (1961) found an average of 75 parasitoids per host with a maximum of