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The Biology and Ecology of Parasitoid Wasps of Predatory Arthropods

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Abstract

Parasitoid wasps are important components of insect food chains and have played a central role in biological control programs for over a century. Although the vast majority of parasitoids exploit insect herbivores as hosts, others parasitize predatory insects and arthropods, such as ladybird beetles, hoverflies, lacewings, ground beetles, and spiders, or are hyperparasitoids. Much of the research on the biology and ecology of parasitoids of predators has focused on ladybird beetles, whose parasitoids may interfere with the control of insect pests like aphids by reducing ladybird abundance. Alternatively, parasitoids of the invasive ladybird *Harmonia axyridis* may reduce its harmful impact on native ladybird populations. Different life stages of predatory insects and spiders are susceptible to parasitism to different degrees. Many parasitoids of predators exhibit intricate physiological interrelationships with their hosts, adaptively manipulating host behavior, biology, and ecology in ways that increase parasitoid survival and fitness.

1. INTRODUCTION

Primary hyperparasitoid: a (koinobiont endo-) parasitoid that oviposits inside the larvae of another parasitoid that is in turn developing inside the body of a secondary herbivore host

The study of multitrophic interactions is embedded in our understanding of community ecology and ecosystem functioning (58, 77, 122). Many of the best-studied multitrophic associations involve plant–insect herbivore–natural enemy interactions (129). Among the most important insect natural enemies are parasitoid wasps (Hymenoptera), which are often ubiquitous components of multitrophic interactions and ecological communities (53, 105). Parasitoids develop on or inside the bodies of other organisms (often other insects); the adults are free living and feed primarily on nectar or pollen, although some host-feed as well (52, 72). Because the development of parasitoid eggs and larvae is restricted by the ostensibly finite resources contained in an individual host, they are considered as model organisms for studying life history, development, and reproductive strategies (59, 71). Moreover, the importance of parasitoids in classical biological control programs in agroecosystems over the past century is well documented (65, 162).

Although studies of food chains in terrestrial food webs involving insects have focused on three levels, these food chains do not necessarily stop there and may extend to four or even more trophic levels (63). For example, the larvae and pupae of many parasitoids of insect herbivores are attacked by primary hyperparasitoids and secondary parasitoids, respectively (117). Hyperparasitoids are important components of plant–insect food chains, and their role in structuring insect communities has received considerable attention and has been reviewed several times in this journal (117, 144, 145). However, other natural enemies in the third trophic level may also harbor parasitoid assemblages. For instance, a diverse range of predatory insects and other arthropods such as ladybird beetles, hoverflies, lacewings, ground beetles, and spiders are also hosts to parasitoids. Because of the importance of some of these predators in mediating trophic cascades in natural communities and in biological control, increasing attention is being paid to their parasitoids to highlight both the applied and fundamental importance of these interactions.

In this review, we synthesize studies examining various aspects of the biology and ecology of parasitoids of predatory arthropods. The review begins with a detailed section examining various aspects of the biology and ecology of parasitoids of ladybird beetles, particularly those of the parasitoid wasp *Dinocampus coccinellae*, which has been the most comprehensively studied. We report on studies describing parasitoid guilds of different developmental stages of ladybird beetles. Lastly, we examine in this section how some parasitoids manipulate ladybird development and behavior in ways that optimize parasitoid fitness. In the subsequent sections, we address similar areas with parasitoids of other predatory insects such as hoverflies, lacewings, ants, and ground beetles. In the next-to-last section, we discuss parasitoids of spiders, including parasitoids that attack spider eggs, egg sacs, juveniles, and adults. We also describe host location strategies in parasitoids and how antagonistic encounters with spiders have led parasitoids to evolve strategies to overcome spider behavioral defenses. The adaptive manipulation of spider web-building behavior is also discussed. We conclude by discussing the role of parasitoids of predatory arthropods in biological control from both positive and negative perspectives and suggest avenues for future research. In this review, we only include non-stinging parasitoids within the Parasitica (68). Some stinging wasps in the Aculeata that also use spiders as hosts (e.g., Pompilidae) are also often described as parasitoids (i.e. 99, 141). However, for the sake of clarity, we exclude pompilids from this review.

2. PARASITOIDS OF PREDATORY LADYBIRD BEETLES

Most species in the large family Coccinellidae, which contains more than 6,000 species in approximately 360 genera, are predators of Sternorrhyncha (aphids, scale insects, whiteflies, and stinkbugs), but some species feed on other prey (e.g., caterpillars, ants, and mites), and some are

phytophagous or omnivorous (51). They are important biological control agents of aphids and coccids, in particular, which are more effectively controlled than aphids (32).

2.1. Parasitoids of Different Ladybird Beetle Life Stages

Parasitism of ladybird eggs is rare and appears to be restricted to phytophagous ladybird hosts in the Epilachninae by several eulophid parasitoid species (17). Because cannibalism among newly hatched carnivorous ladybird larvae is often high, the risk of predation of parasitized eggs is also high and has reduced selection for such interactions to evolve (17). Larval and pupal stages of predatory ladybird beetles are the most vulnerable stages to attack by parasitoids (19). The best-studied larval parasitoids are in the genus *Oomyzus* (Eulophidae: Tetrastichinae), particularly *Oomyzus scaposus*, which has a wide distribution and has been described as the most common parasitoid associated with ladybird beetles (19). Larvae of *Oomyzus* species are gregarious, and brood sizes tend to increase with increasing size or later instar of the host at the time of parasitoid oviposition (39, 139). Hymenopteran parasitoids are haplodiploid, with unfertilized eggs developing into males and fertilized eggs developing into females, and parasitoid mothers are able to control the sex of their offspring (27, 52). Sex ratios of both *O. scaposus* and *Oomyzus spiraculus* are highly female biased irrespective of host size or instar at parasitoid oviposition (39, 139). This suggests that the species are engaged in local mate competition in which just enough sons are produced to mate with the daughters (131). The genus *Homalotylus* (Encyrtidae) contains larval and pupal parasitoids that are specialized on parasitizing coccinellids (19). Species attacking small or early host stages are solitary, whereas those attacking large or late stages are gregarious (80). In a study of the gregarious *Homalotylus eytelweinii*, brood sizes increased with instar at parasitoid oviposition, but adult emergence was higher when early instar hosts were parasitized (57). This suggests that various life history traits are differentially affected by host instar at the time of parasitoid oviposition.

Other larval and pupal parasitoid species of ladybird beetles belong to the Chalcididae (e.g., *Ulga* species), Encyrtidae (genus *Cowperi*), Proctotrupidae (genus *Nothoserphus*), Pteromalidae, and Eulophidae (19). Detailed information on various aspects of the taxonomy and biology of these parasitoids has been provided in other, earlier reviews (17, 19).

2.2. Interaction Between Ladybird Beetles and *Dinocampus coccinellae*

Interactions between the cosmopolitan parasitoid *D. coccinellae* (Braconidae: Euphorinae) and its coccinellid hosts have been disproportionately well-studied. It is a solitary endoparasitoid of adult ladybird beetles mainly belonging to the subfamily Coccinellinae (19). Although it prefers to parasitize adult ladybird beetles, it may also parasitize pupae and larvae when adults are scarce (47). However, immature parasitoid larvae delay their development in immature ladybird stages and only egress from the imago (73). This host stage preference is considered to be adaptive because parasitism is more successful and development time is shorter when hosts are parasitized in the adult stage (109). Females can parasitize and successfully develop in a range of host species (54 reported species; 17, 18, 19) but have a preference for and are more successful in larger individuals, both across and within species (90, 123, 157). Moreover, *D. coccinellae* prefers to parasitize female over male hosts (12, 15, 96), even when correcting for size (25). This has been attributed to the fact that female hosts have a greater resource intake than male hosts and thus produce larger progeny (25). In addition, preference and performance are higher in young, newly egressed adults than in older adults emerging from diapause (96). The ability of *D. coccinellae* to discriminate between parasitized and unparasitized hosts is poorly developed and/or transient (111), as shown by the fact that rates of superparasitism in their hosts in the field can exceed 60% (16).

Endoparasitoid: a parasitoid that oviposits into the body of the host and whose larvae develop by feeding internally on host hemolymph and fat body

Superparasitism: parasitism of a host that has already been parasitized by the same (i.e., self) or another (i.e., conspecific) female parasitoid of the same species

The larvae of *D. coccinellae* feed on teratocytes (73, 135), trophic cells that are released in the host hemocoel upon larval hatching and absorb nutrients from the host haemolymph (143) and fat body (135). Teratocytes are only produced by some parasitoid clades and also play a role in immunosuppression (143). Reduced production of these cells may compromise parasitism success in some host species such as *Harmonia axyridis* (42). Interestingly, adult ladybird hosts often survive parasitism and are able to reproduce successfully (103). Allowing the host to remain alive and active following parasitoid egression is adaptive when it increases parasitoid survival, for instance, when the parasitoid manipulates the behavior of the host to provide protection against parasitoids and predators (61, 102; see also Section 2.3).

To locate hosts over short distances, *D. coccinellae* relies on visual and olfactory cues (2, 112, 123). Movement of the host is the initial cue attracting female parasitoids, which explains why mobile hosts are often attacked more frequently than are inactive ones (11). Movement also facilitates parasitism by exposing the preferred site of oviposition on the host (123), where tissues are softer, allowing easy penetration by the ovipositor (123, 135); this site may vary with host species (112). Volatiles secreted by a gland under the ladybird coxae play a role in host recognition but do not seem to be important for oviposition to take place (123). Aposematically colored ladybird beetles have a distinct smell and, upon attack, excrete a fluid containing toxic alkaloids that function as a defense against predators (24). An extract of adult *Coccinella septempunctata*, as well as a pure alkaloid isolated from this extract that elicited a strong electrophysiological response in electroantennogram assays, was attractive to *D. coccinellae* in an olfactometer (2). These results suggest that host-derived chemicals play an important role in the steps leading up to host acceptance. However, the exact identity and source of the chemicals mediating each of the steps are not clear (whether volatile, contact, or those excreted upon attack) (96).

Dinocampus coccinellae has also been studied for its ability to control *H. axyridis*. This ladybird species has been widely introduced as a biological control agent, but due to its harmful effects on native coccinellids and adverse effects on human health and fruit production, it is now considered invasive in many parts of its introduced range (11, 14). Several studies have shown that *H. axyridis* is a poor host for *D. coccinellae*, and therefore, the effectiveness of this parasitoid to control this invasive species is limited (11, 22, 26, 31, 67, 127). Field observations of rates of parasitism of *H. axyridis* by *D. coccinellae* vary between 0% and 30%, whereas rates can reach up to almost 50% for other coccinellid hosts (18). Multivoltine parasitoid species, such as *D. coccinellae*, must synchronize their active period with that of their hosts (16), whose availability in turn depends on that of the host's prey. As a result of this and other factors, levels of parasitism may also vary over the course of a growing season (115, 138, 150). Host dissections showed that, in the field, parasitism rates of *H. axyridis* and *Coleomegilla maculata*, a native ladybird species in North America, were similar (67), but due to reduced host suitability, the rate of emergence of adult parasitoids from the former species is much lower (42). This result suggests that, in the field, *D. coccinellae* may not be able to discriminate between suitable and less suitable host species (67). Alternatively, in the field, *D. coccinellae* may also attack larval stages of *H. axyridis*, which are less aggressive (43) and more suitable for offspring development and survival (11, 43). Recent data suggest that populations of *D. coccinellae* in central Europe are overcoming host immunity: Parasitism rates of *H. axyridis* were found to be as high as 46% (83), which is remarkable given parasitism rates in its native range of 7.5% or less (18).

2.3. Host Behavioral Manipulation by Ladybird Parasitoids

Interactions between parasitoids and their hosts are profoundly intimate and frequently involve an array of changes in the biology, ecology, and behavior of hosts that are mediated by the parasitoid

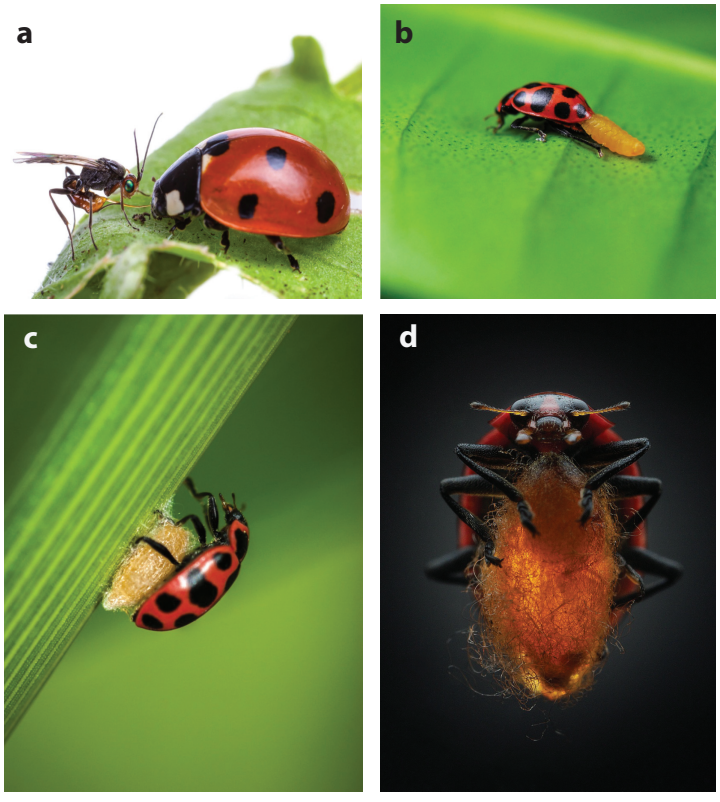

Figure 1

(*a*) Adult female *Dinocampus coccinellae* ovipositing into adult ladybird beetle (*Coccinella septempunctata*). (*b*) Mature larva of *D. coccinellae* egressing from adult ladybird beetle (*Coleomegilla maculata*). (*c*,*d*) Previously parasitized adult *C. maculata* beetle sitting atop cocoon of *D. coccinellae*. Photograph in panel *a* courtesy of Hans Smid (**http://bugsinspace.nl**). Photographs in panels *b* and *c* courtesy of Mathieu Bélanger Morin. Photograph in panel *d* courtesy of Anand Varma (**https://www.varmaphoto.com/**).

mother or her offspring (9). Endoparasitic koinobionts in a small number of braconid subfamilies exhibit adaptations whereby their hosts become phenotypic extensions of the parasitoids through some form of physiological manipulation (1). In this case, parasitized hosts are not killed during parasitism, but instead remain alive for up to several days after the mature parasitoid larvae egress, construct cocoons, and pupate (59). The zombified hosts thereafter act as bodyguards for the parasitoid cocoons, defending them against generalist predators or hyperparasitoids (56, 61). One of the best-studied host–parasitoid associations examining redirection of host behavior toward parasitoid cocoon guarding involves *D. coccinellae* and its ladybird host, *C. maculata* (101–103). The parasitoid female oviposits into adult ladybird beetles (**Figure 1*a***), and the larvae primarily feed on host haemolymph and fat body before egressing from the abdomen of their host (**Figure 1*b***). The parasitoid then spins its cocoon, after which the ladybird wraps its appendages around it, apparently shielding it from potential predators and hyperparasitoids (**Figure 1*c*,*d***). Many ladybird beetles biosynthesize alkaloids, which act as repellents against predators (24), making ladybird beetles effective bodyguards for their parasitoids. As in many species that sequester or synthesize toxins in their body, ladybird beetles are aposematically colored and thus advertise their toxicity to natural enemies (146). Host behavioral manipulation appears to be mediated by an RNA virus,

Koinobiont: a parasitoid that attacks hosts that continue to feed and grow during the course of parasitism, only arresting host development just prior to parasitoid pupation

injected by the parasitoid female into the host at oviposition (29). This virus replicates in the host's nervous tissues, inducing neuropathological changes that affect behavior (29).

3. PARASITOIDS OF HOVERFLIES

Adult hoverflies (Syrphidae: Diptera) feed on nectar and pollen and are important pollinators of flowering plants in wild and agricultural ecosystems. The larvae are insectivorous, feeding on aphids and some other Homoptera (whiteflies and leafhoppers). Thus, both life stages provide important ecosystem services in agricultural systems (34).

The adult stages of many hoverfly species are mimics of stinging wasps and bees, reducing their risk of becoming prey themselves. However, the immature stages of syrphid flies are attacked by a range of hymenopteran parasitoids in the families Diplazontinae (Ichneumonidae), Figitidae (Cynipoidea), Encyrtidae and Pteromalidae (Chalcidoidea), and Megasplidae (Ceraphronoidea) (44, 74, 130). Species in the subfamily Diplazontinae are generally associated with Syrphidae (81), with the exception of the cosmopolitan *Diplazon laetatorius*, which has a broad host range (75, 164) and is also frequently recovered from parasitized hoverflies (44, 55, 70). Species in this subfamily are koinobiont parasitoids, attacking egg or early larval stages of their host and egressing as adults from the pupae (44).

The genus *Pachyneuron* (Chalcidoidea: Pteromalidae) contains species that are hyperparasitoids of parasitoids of sap-sucking insects, as well as primary and hyperparasitoids of their predators, including syrphid flies, coccinellid beetles, and chrysopids (lacewings) (49). It is not clear which host stage(s) these wasp species parasitize, but the pupae or cocoons are likely to be the most vulnerable (49).

Parasitism rates of syrphids in agricultural fields have been found to range from 5% to 45% (136), and parasitism by *D. laetatorius* alone can reach levels of more than 20% (70). Parasitoids of syrphids often attack more than one host species, i.e., they are considered generalists, although their host range may be overestimated (128).

4. PARASITOIDS OF LACEWINGS

Green (Neuroptera: Chrysopidae) and brown (Neuroptera: Hemerobiidae) lacewings are beneficial insects in agroecosystems, especially in orchards (142). The larval stages are carnivorous and feed on plant-sucking arthropods, such as aphids, soft scales (Hemiptera; Coccoidea), and mites, as well as other soft-bodied insect life stages (e.g., eggs and early larval stages) (142). Adults of brown lacewings and those of green lacewings in the genus *Chrysoperla* are omnivorous, whereas all other adult green lacewings are nonpredacious (28). Green lacewing species in the genera *Chrysopa* and *Chrysoperla* are most commonly used in integrated pest management programs, particularly species of the *Chrysoperla carnea* complex (common green lacewings), which are also frequently found in field crops (142). *Chrysoperla carnea* sensu latu is the best-studied lacewing species and is an important predator used in greenhouses. It is thus not surprising that most of the known lacewing parasitoids are those associated with this species.

Egg parasitoids of chrysopids predominantly belong to the genus *Telonomus* (Scelionidae) (3, 48, 76). In addition, *Trichogramma atopovirilia* (Trichogrammatidae) and *Myartsevaia chrysopae* (Encyrtidae) have been recovered from chrysopid eggs in Mexico (121), where the control of *Melanaphis sacchari* (sugarcane aphid) largely relies on the release of *C. carnea*. *Trichogramma* species are often used to control lepidopteran pests (137, 167), but parasitism of nontarget hosts, such as egg stages of lacewing predators, may reduce biological control efficacy when trichogrammatid host fidelity is limited or modified under field conditions (132).

Larval stages of chrysopids are predominantly attacked by chalcidoid parasitoids, e.g., *Catolaccus* sp. (Pteromalidae), *Tetrastychus* sp. and *Isodromus* sp. (Eulophidae), and *Perilampud* sp.

(Perilampidae) (3, 48, 76, 151). Perilampid species lay eggs in prey patches of their hosts. The first peripampid larval stage is free living (planidia) and externally attaches itself to the lacewing host larva, whereas the other parasitoids oviposit directly into the body of the host (48). The trophic status of perilampid species is not always clear, although they are often referred to as hyperparasitoids (3). Identified pupal parasitoids of *Chrysoperla* include *Baryscapus* sp. (Eulophidae) and *Gelis ilicicolator* (Ichneumonidae) (3, 76). Species in the genus *Chrysopophthorus* (Braconidae) are koinobiont endoparasitoids of adult green lacewings (3, 154). Interestingly, as in some adult parasitoids of ladybird beetles, the chrysopid host may survive, and females may continue to lay eggs after the *Chrysopophthorus* parasitoid larva has egressed (154). Parasitism rates of chrysopids in the field are highly variable but can reach levels of up to 80%, predominantly by *Tetrastycus* and *Telenomus* species, depending on biogeographical region (3, 48, 76).

Parasitoids of brown lacewings have been little studied. One exception is *Anacharis zealandica* (Figitidae), a solitary larval koinobiont endoparasitoid of the Tasmanian lacewing *Micromus tasmaniae*, which is an important predator of aphids in grasslands and on vegetable crops in Australia and New Zealand (69, 126). These studies demonstrated that the addition of floral resources can be used as an alternative resource for this omnivorous lacewing but can also provide nectar to *A. zealandica* parasitoids and increase their numbers. Interestingly, the addition of flower resources only affected biological control (negatively) at high aphid densities and not at low densities, showing that these multitrophic interactions are complex and context dependent.

5. PARASITOIDS OF PREDATORY GROUND BEETLES

Ground beetles (Carabidae) are a very well-studied family in the Coleoptera, with over 40,000 described species worldwide (94). They are abundant in most terrestrial habitats, including cold polar regions (94). The larvae and adults of most species are predators of other invertebrates, although some species are omnivorous as adults and may feed on plant materials like seeds and pollen (94). Many species are considered to be important as generalist predators in biological control programs against a range of pests (95).

Very little is known about egg parasitoids of carabids. Females of certain species in the genera *Dicaelus*, *Chlaenius*, and *Galerita* lay their eggs in mud or clay cells above the soil (79). Their eggs have been found to be parasitized by *Hoplogryon* (Scelionidae, Teleasinae). A common egg parasitoid of *Chlaenius* species is *Prosacantha caraborum* (Scelionidae) (79). Parasitoids in the Proctotrupidae are larval endoparasitoids that are often associated with Carabidae and other soil arthropods (149). In general, females in this family are wingless and dwell in the soil. Given that these parasitoids are efficient soil excavators, parasitism of carabid larvae most likely occurs in the host's burrow (23). The most common parasitoids of carabids in this family are the gregarious *Phaenoserphus viator* and the solitary *Phaenoserphus pallipes*, which have been recovered from *Pterostichus* and *Notiophilus* species (23, 149). Levels of parasitism by these species can reach 25% (23). Parasitism of adults is rare. For instance, in a study of parasitoids of adult riparian carabid beetles in the genus *Bembidion*, no hymenopteran parasitoids were found (4). The described parasitoids of adult carabid stages are braconid wasps in the genus *Microtomus*, which emerged from field-collected *Harpalus rufipes*, of which the larvae are herbivorous and the adults omnivorous, and carnivorous *Galeritus* sp. (23, 66, 125).

6. PARASITOIDS OF PREDATORY ANTS

Many species in the Formicidae are ground-dwelling predators or scavengers of arthropods. Some species may attack humans and livestock (e.g., *Solenopsis* sp.) (33). Ants often supplement their diet

with plant tissues and honeydew (163). Given their omnipresence and often broad dietary breadth, ants can be important biological control agents of agricultural pests (33, 163). However, some ant species require relatively high densities of honeydew-producing Hemiptera (Sternorrhyncha families) to supplement their energy needs and may feed on other beneficial arthropods.

Species in two hymenopteran parasitoid taxa have well-established relationships with ants: the family Eucharitidae (Chalcidoidea) and the tribe Neoneurinae (Braconidae) (38, 91). There are parasitoids of ants in other hymenopteran taxa, but the evidence demonstrating that they are true parasitoids of ants, and not parasitoids of myrmecophilous arthropods, is circumstantial (91). Eucharitid wasps parasitize larvae of ants in 53 genera distributed over three families (Oraseminae, Eucharitinae, and Gollumielinae) (91). Most eucharitids have a host range restricted to a single genus. Females deposit their tiny eggs singly (*Oresema*) or in clusters of up to 10,000 eggs (*Stilbula tenuicornis*) in or on specific plant tissues (leaves, buds), depending on the species (20). The first-instar larvae, or planidea, actively seek worker ants or prey of ants and use phoresy for transportation to the ant nest, where they attack mature larvae and pupae and develop as endo- or ectoparasitoids (91). They egress as adults from the host pupa and avoid detection by the ant by active or passive chemical mimicry of ant colony odors (91). Worker ants may even assist the adult to egress from the cocoon or remove partially opened cocoons from the nest without attacking them (7). Species in the tribe Neoneurinae are koinobiont endoparasitoids that attack adult worker ants and develop in the abdomen of their host (91). Full-grown *Elasmosoma* sp. larvae exit the host, often through the host anus, and pupate in the soil (118). Parasitism rates are highly variable but can reach levels up to 70% or higher for some parasitoid species (91).

Phoresy: an association whereby one organism disperses while attached to the body of another organism, which generally confers no fitness costs to the host

Ectoparasitoid: a parasitoid that attaches its egg(s) externally to the host at oviposition and whose larvae feed externally on host tissues

Idiobiont: a parasitoid that attacks non-growing host stages, such as eggs or pupae, or that permanently paralyzes the host, keeping host resources static throughout the interaction

7. PARASITOIDS OF SPIDERS

Spiders are among the most important and ubiquitous of terrestrial predatory arthropods (108). Currently, there are almost 50,000 described spider species from 129 families (30). With few exceptions, spiders are all predators of other invertebrates, and even small vertebrates (108, 124). They occur in a huge variety of habitats (153) and are considered to be important in biological control programs (124).

Although the vast majority of hymenopteran parasitoids attack other insects, a small number of parasitoid families contain species whose larvae are solitary or gregarious idiobionts and koinobionts that develop on or inside the eggs, juveniles, or adults of spiders. Most hymenopteran parasitoids of spiders are highly specialized and do not exploit other hosts (45). In this section, we discuss egg and egg sac parasitoids and parasitoids of juveniles or adults separately.

7.1. Parasitoids of Spider Eggs and Egg Sacs

The parasitoids of spider eggs and egg sacs that have been described come from only a few families. They exploit their host eggs in two quite distinct ways. In the first group, females are idiobionts that probe through the thin silk of spider egg sacs and oviposit into individual spider eggs that are clustered within the sacs. The parasitoid larvae develop solitarily within the eggs and emerge as adults by perforating the egg chorion. Species of solitary parasitoids in the family Platygastridae (subfamily Sceliioninae), such as *Idris flavicornis*, *Ceratobaeus* spp., and *Baeus* spp., and Eurytomidae (subfamily Eurytominae), such as *Philolema latrodecti*, are known to attack the eggs of spiders in several families, including the Lycosidae, Theridiidae, Segestriidae, and Desidae (6, 35, 78, 98, 114, 120). Little is known about the biology, development, or behavior of most spider egg parasitoids. An early study found that *Idris* sp. preferred younger over older egg sacs of the wolf spider, *Pardosa lapidicina* (35), and responded to silk odors of the host egg sac with vigorous tapping movements

of its antennae. This study also found that eggs close to the periphery of the egg sac were more susceptible to parasitism than eggs clustered in the center. By contrast, females of the platygastrid wasp *Ecthrodesis laorali* parasitized every egg in egg sacs of the intertidal spider, *Desis formidabilis*, when they were able to locate and exploit them but preferred microhabitats where its host was most abundant (114). As in many primary parasitoids of herbivorous insects, *E. laorali* and *Ceratobaeus* spp. are protandrous, and their offspring sex ratios are heavily biased in favor of females (5, 114, 156). This suggests that, when a female parasitizes multiple eggs within a single egg sac, the earlier-emerging males mate with female siblings under conditions of local mate competition (110).

The second group consists of parasitoids whose larvae attack multiple eggs simultaneously inside of fully cocooned egg sacs. The majority of these parasitoids are from the family Ichneumonidae (subfamily Cryptinae), although this behavior has also been observed in *Pteromalus platyphilus* (Pteromalidae) (45). Species in these clades are ectoparasitic idiobionts, and some species are also secondary hyperparasitoids of primary parasitoid cocoons (119). By far the most important parasitoids of spider egg sacs are in the genus *Gelis*; members of this genus have been recorded in egg sacs of spiders in several families, including Linyphiidae (155), Lycosidae (8, 21, 37), Agelendiae (8), Zodariidae (87), and Theridiosomatidae (89). Females perforate the thin silk of the egg sacs and lay their egg(s) directly onto the surface of the clustered eggs within them. After hatching, the parasitoid larvae feed externally on the eggs and may kill most but not necessarily all of them, although the number killed depends on the relative size of the parasitoid and the egg sac of the spider (13, 35). Most species of *Gelis* are wingless and mimic ants chemically, behaviorally, and morphologically (62). Despite lacking wings, they are apparently capable of parasitizing egg sacs of spiders that have been suspended via threads (89). For example, *Gelis agilis* females descend head-first down single threads of silk to reach the cocoons of the primary parasitoid *Meteorus pulchricornis* suspended at the end of them (60). Adult geline females, which attack primary parasitoid hosts, generally have very low fecundity (158) and produce large, yolky anhydropic eggs (92) that require proteins that are generally obtained by host-feeding by the adult female wasps (72). Although host-feeding from egg sacs has not yet been observed from gelines, it is likely that it also occurs. Other cryptines (i.e., *Bathytrix brunnea*, *Trychosis cyperia*) have occasionally also been reported as egg sac parasitoids of spiders (45, 107).

As with parasitoids of spider eggs, the biology and ecology of spiders that produce egg sacs have been little studied. It has been argued that spiders have evolved ecophysiological strategies related to the structure and placement of their egg sacs to resist attack from natural enemies (6). Some spiders even guard their egg sacs against predators and parasitoids (41). However, while these strategies are effective against many generalist predators, such as ants, strong reciprocal selection among specialist parasitoids has led them to become highly efficient at locating and exploiting unattended egg sacs of their spider hosts (6). For example, host searching behavior of *Gelis fenestrans*, a specialist parasitoid of egg sacs of the linypiid spider *Erigone atra*, was affected by both plant and host-related odors. In Y-tube experiments, parasitoids preferred odors of wheat over grass and were strongly attracted to silk from *E. atra* but not to silk of three other species of linyphiids, suggesting strong host specificity (155). Another solitary cryptine, *T. ciperia*, is a specialist egg sac parasitoid of the crab spider, *Misumena vatia* (Thomisidae), and parasitoid larvae invariably consume all of the host eggs before pupation. In this interaction, spider host egg mass was positively correlated with adult female, but not male, parasitoid size, although females were larger at eclosion and utilized host resources more efficiently than males (107). Offspring sex ratios of *T. ciperia* from field-collected egg sacs were also female biased. These admittedly limited data reveal that spider egg sac parasitoids exhibit traits (e.g., sexual size dimorphism, female-biased sex ratios) similar to those of hyperparasitoids and primary parasitoids of herbivorous hosts (52, 59).

Protandrous: species in which male parasitoids emerge earlier than sibling and nonsibling females from a host patch that facilitates mating when this is time limited

Secondary parasitoid: also known as a pseudohyperparasitoid; a (idiobiont ecto-) parasitoid that lays its egg on or inside the prepupae or pupae of a primary parasitoid within its preconstructed cocoon

Figure 2

(*a*) Adult female *Sinarachna pallipes*. (*b*) Mature larva of *S. pallipes* feeding on adult araneid spider, *Eustala anastera*. (*c*) Cocoon of *S. pallipes* suspended in the web of *E. anastera*. The hole in the top of the cocoon indicates that an adult parasitoid has recently emerged. (*d*) Prey capture orbicular web of the araneid *Cyclosa conica*. (*e*) Highly modified web of *C. conica* parasitized by *Zatypota picticollis*. Photographs in panels *a–c* courtesy of John Maxwell (**https://bugguide.net/node/view/401720**). Photographs in panels *d–e* courtesy of Stanislav Korenko.

This suggests that selection pressures affecting the expression of traits are similar across parasitoids in different trophic levels.

7.2. Parasitoids of Juvenile and Adult Spiders

Juvenile and adult spider stages are also attacked by a small but highly specialized group of parasitoids in the *Polysphicta* group (45) (**Figure 2*a***). This is a monophyletic lineage of solitary koinobiont ectoparasitoids in the Pimplinae (Ichneumonidae), which contains approximately 190 parasitoid species from 21 genera (46). These parasitoids attack spiders in several families including the Agelenidae (100), Araneidae (36, 54, 82), Dictynidae (84), Tetragnathidae (85), and Theridiidae (40, 86, 148). Host specialization among polysphinctine species occurs at the spider family or even species level (88).

Recent studies have shed considerable light on the complex biology and behavior of these parasitoids. Attack behavior varies among different parasitoid species and involves both host subjugation and mitigation of spider defenses. Direct parasitoid attacks have been observed on spiders resting in exposed locations on the web (36), whereas protracted pursuits may occur when spiders are protected by silk threads in more structurally complex webs or when they escape inside retreats (54). In the latter case, the parasitoid female may adopt a sit-and-wait strategy until the spider leaves its retreat and the pursuit recommences (82). During the oviposition sequence, female parasitoids first inject venom into their spider host, paralyzing it for several moments (82, 165). Host envenomation sometimes requires precise and repeated insertions of the ovipositor into the spider's mouth, presumably reaching the subesophageal ganglion (82). The ovipositors of polysphinctine parasitoids are uniquely adapted for laying eggs onto the antero-lateral dorsal section of the spider's abdomen (147). In some species, the first-instar parasitoid larva remains inside the egg chorion, whereas later instars produce saddles on their seventh or eighth abdominal segments that anchor them to the host abdomen (**Figure 2*b***). The larvae also possess hook-like appendages that are used to hold the silk lines of their host (165). Like egg-sac parasitoids in the Cryptinae and most other pimpline ichneumonids, polysphinctine wasps produce large, anhydropic eggs that presumably require exogenous proteins obtained via host-feeding behavior (72), although this has not yet been described in these parasitoids. During parasitism, the spider host continues foraging and web-building as usual (88). Once the parasitoid larva enters its final instar, it consumes most host tissues, avoiding only sclerotized portions of the spider body (e.g., appendages, cephalothorax). At this point, the mature parasitoid larva spins its cocoon on its host's web. In host spider species where there is pronounced sexual size dimorphism (i.e., large females

and dwarf males), female parasitoids tend to reject male spiders for oviposition because the limited amount of biomass on small hosts decreases offspring size, and thus fitness (86).

7.3. Host Behavioral Manipulation by Polysphinctine Parasitoids

As described above for ladybird beetles, some primary parasitoids manipulate the behavior of their hosts before killing them, turning them into bodyguards. Similarly, polysphinctine parasitoids manipulate the ecology and web-spinning behavior of their hosts to optimize their survival to eclosion. In some species, the parasitoid also induces overwintering behavior in its spider host and completes its development the following year (86). After parasitism, *Zatypota* sp. induces juveniles of the social theridiid spider, *Anelosimus eximus*, to disperse from communal webs and construct entirely new webs made up of much denser silk with limited openings, giving reduced access to predators or hyperparasitoids (40). Isolation from the communal web is presumably adaptive because it reduces the risk of the adult parasitoid being attacked by other *A. eximus* spiders at eclosion. Another parasitoid, *Brachyzapus niookensis*, induces its host, the funnel-web-building spider, *Agelena limbata*, to lay additional threads (or veils) of both fine and dense silk that cover the spider and protect the entrance of the funnel against generalist predators such as ants (100). The most intricate form of regulation among polysphinctines is documented among parasitoids of spiders that build orbicular webs. Species in several genera (e.g., *Zatypota*, *Reclinervellus*, *Polysphincta*) induce their araneid spider hosts to construct highly modified webs that differ dramatically from the capture webs of healthy spiders. The modified cocoon-webs spun by parasitized spiders use the pre-existing frame lines of the capture webs but lack its characteristic orb and contain a single, strong central thread on which the parasitoid either anchors or suspends its cocoon (**Figure 2*c–e***). This apparently reduces the accessibility of the parasitoid to predators and perhaps hyperparasitoids. Changes in spider web-spinning behavior either are caused by chemicals injected into the host by the adult female parasitoid during oviposition or are introduced into the spider body by parasitoid larva early in the larva's development. When older parasitoid larvae are artificially removed from their spider hosts, the spiders will nevertheless construct altered cocoon webs (36), indicating that the behavioral change is persistent.

8. DISCUSSION AND FUTURE PERSPECTIVES

The ecology and biology of parasitoids of arthropod predators have received little attention, with the exception of a few systems such as the ladybird parasitoid *D. coccinellae* or *Zatypota* spp. parasitoids of spiders. Most papers on these parasitoids have focused on taxonomy and phylogeny. All predator groups reviewed in this article have parasitoids that are often highly specialized and thus are confined to specific families or genera of predatory hosts. This is particularly true for parasitoids of spiders and ants and can be explained by unique aspects of the biology of these predators. The factors that mediate foraging behavior of parasitoids of arthropod predators in natural environments have to date received little attention. Herbivore-induced plant volatiles are important foraging cues for parasitoids of insect herbivores (152). As the prey of ladybird beetles, hoverflies, and lacewings are herbivorous, prey-induced plant volatiles may also provide reliable cues to guide the parasitoids of these predators to their hosts. For instance, Orre et al. (113) showed that *A. zealandica* (Figitidae), a parasitoid of lacewing larvae, was attracted to traps baited with methyl salicylate, a ubiquitous compound in volatile blends emitted by plants in response to herbivory (116). Alternatively, host location may largely be mediated by direct cues related to the prey of the predator. There is some evidence that hoverfly larvae that have depleted a prey colony rely on aphid-related cues (e.g., honeydew), and not on plant-related cues, to find new prey patches on other plants (160). Females of ladybird beetles, lacewings, and hoverflies lay their eggs near aphid

colonies and may use aphid-derived cues such as honeydew and/or aphid alarm pheromones when locating suitable oviposition sites (161). As prey abundance and colony size are determined by food plant quality, the host plant may only indirectly play a role in this case. How parasitoids of many other arthropod predators find their hosts is even less known.

Ladybird beetles, hoverflies, and lacewings are important biological control agents of aphids, which cause serious economic losses in agriculture not only via their feeding damage, but also by vectoring plant viruses. This may explain why these predators, particularly ladybird beetles, have been relatively well studied, although the importance of ants, ground beetles, and spiders in controlling agricultural pests is increasingly being recognized (10, 33, 166). Some aphid species are myrmecophiles and have evolved a mutualistic relationship with ants, in which ants protect aphids against their enemies in return for energy-rich resources in the form of honeydew (97, 140). Ants and aphid predators may engage in competitive interactions, especially when prey is scarce (97), and some species of aphid predators have evolved specific behavioral, morphological, or chemical

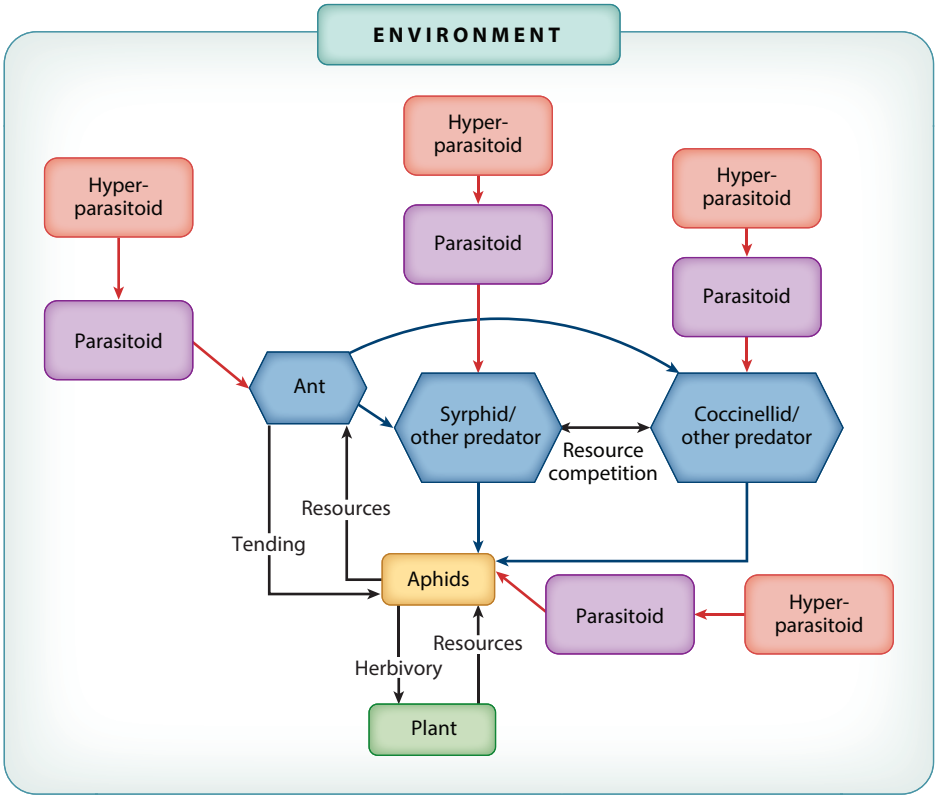

Figure 3

Aphid food web extended to the fifth trophic level. Different colors refer to the various trophic levels or natural enemy status [predators in blue and (hyper)parasitoids in purple and red], with the plant (first trophic level) in green and aphids (second trophic level) in yellow. Parasitoids of aphids are in the third trophic level, whereas those of aphid predators are in the fourth. All parasitoids can be attacked by their own parasitoids (hyperparasitoids). Direct interactions between food-web members are indicated by arrows, with predation in blue and parasitism in red. Other types of direct interactions are indicated by dark gray arrows. Interactions are not restricted to direct ones, but for simplicity, indirect interactions are not considered in this figure. Figure adapted with permission from Reference 50.

traits that facilitate their ability to live in the vicinity of aphid-attending ants (64, 97, 104, 106, 134, 159), which may even provide an enemy-free space for the aphid predators or render them less suitable hosts for their parasitoids (133, 134). For instance, the sticky wax filaments on the larvae of the coccinellid *Azya orbigera*, which feed on coccid prey, provided protection against attack by *Azteca instabilis* ants, which were aggressive towards a parasitoid of the coccinellid *Homalotylus shuvakhinae* (Chalcidoidea: Encyrtidae) (93).

The structure of the aphid-predator food web does not end there. As do parasitoids of herbivorous insects, parasitoids of predatory arthropods have their own parasitoid natural enemies. Because predatory arthropods are members of the third trophic level, their primary parasitoids expand the trophic chain to the fourth level, and their hyperparasitoids in turn expand it to the fifth level. Studies on these hyperparasitoids are scarce, but a few studies have included hyperparasitoid records when surveying parasitism of predatory arthropods [lacewings (3), ladybirds (19), and hoverflies (74)]. Interestingly, whereas hyperparasitoids of primary parasitoids of insect herbivores may compromise efficacy of biological control, hyperparasitoids of predator parasitoids may positively affect control by reducing the abundance of parasitoids attacking predacious biological control agents. To what extent this is the case under natural conditions is an open question. Ecological research should investigate species interactions under conditions of increasing complexity, considering all members of the system, to better understand and predict how changes in one compartment of the food web influences others and vice versa. In **Figure 3**, we expand the food web proposed by Gilbert (50) by adding parasitoids and hyperparasitoids of the various members in the food web. We realize that considering all of these components simultaneously may be difficult; however, when focusing only on bi- or tritrophic interactions, one should exercise caution when describing patterns or deriving conclusions if all members of the system have not been considered.

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