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Extrinsic Inter- and Intraspecific Competition in Parasitoid Wasps

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Abstract

The diverse ecology of parasitoids is shaped by extrinsic competition, i.e., exploitative or interference competition among adult females and males for hosts and mates. Adult females use an array of morphological, chemical, and behavioral mechanisms to engage in competition that may be either intra- or interspecific. Weaker competitors are often excluded or, if they persist, use alternate host habitats, host developmental stages, or host species. Competition among adult males for mates is almost exclusively intraspecific and involves visual displays, chemical signals, and even physical combat. Extrinsic competition influences community structure through its role in competitive displacement and apparent competition. Finally, anthropogenic changes such as habitat loss and fragmentation, invasive species, pollutants, and climate change result in phenological mismatches and range expansions within host–parasitoid communities with consequent changes to the strength of competitive interactions. Such changes have important ramifications not only for the success of managed agroecosystems, but also for natural ecosystem functioning.
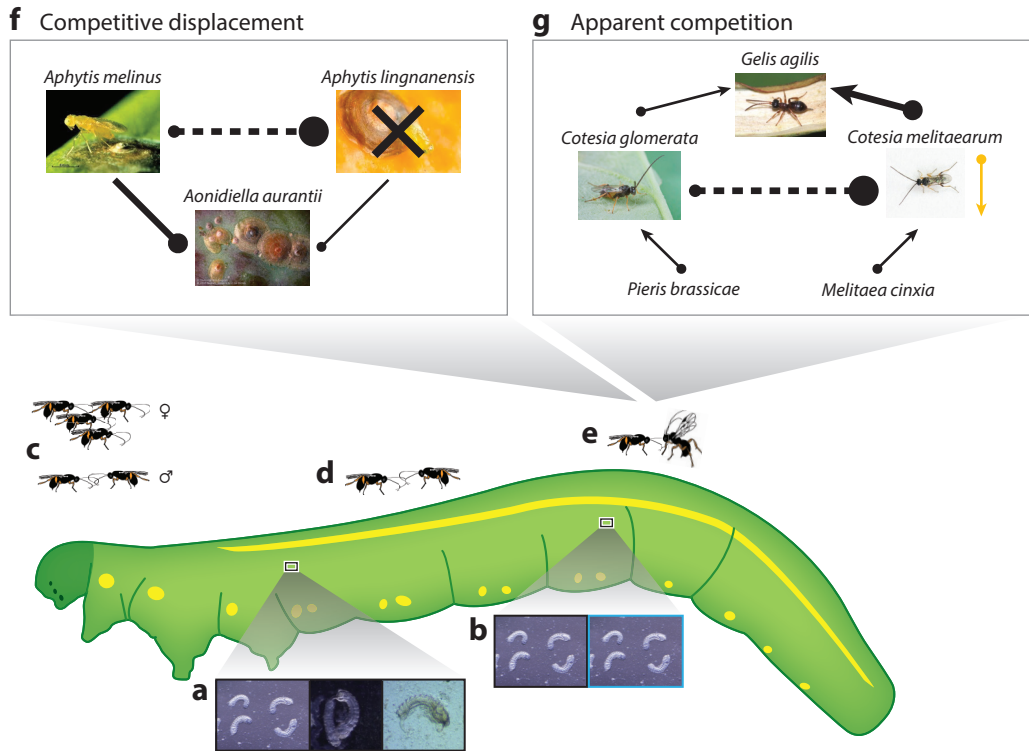
INTRODUCTION

Competition among organisms for vital resources such as food (14, 47, 98), living space (103), refuges from extreme weather conditions or natural enemies (15), and mates (94) has long been a major focus of ecological research. Competition among insects plays a major role influencing life-history evolution, trait expression, niche size, and ultimately the structure and function of ecological communities (98). The intensity of selection is high when two organisms compete for a resource that may be limiting in space and time, such as plant tissues for herbivores, prey for predators, or hosts for parasitoid wasps. While parasitoids are free living as adults, parasitoid larvae obtain all of the resources necessary for development from a single arthropod host (67). Competition among parasitoids, therefore, involves a mixture of both extrinsic (among free-living adults; **Figure 1c–e**) and intrinsic (among developing immatures; **Figure 1a,b**) competition (81). Compared with other consumer guilds, however, parasitoids are especially susceptible to competition for hosts because of two main factors. First, most parasitoids are highly specialized, attacking only one or a few species of hosts in nature (67), leading to increased levels of intraspecific as well as interspecific competition. By contrast, most predators are far less choosy and may attack a range of prey species over the course of their lives (154). Moreover, although most insect herbivores are specialists (108) and thus only feed on one or a few closely related species of plants, competition is reduced by the fact that plants generally contain sufficient biomass to support many herbivores over the course of a growing season, enabling multiple herbivore species to co-occur on the same plant (157). Suitable hosts for parasitoid development are often scarce or distributed very heterogeneously in nature, thereby imposing strong selection pressure on adult females to locate hosts. In turn, adult males often aggregate at female emergence sites or oviposition sites where they engage in strong, sometimes lethal, competition for mates. Second, the total mass of adult parasitoid offspring is often only marginally less than that of the host, resulting in intense competition among parasitoid larvae developing within the same host (80). While they occur at different life stages, intrinsic and extrinsic competition are clearly linked, with extrinsic competition representing the first line of competition among parasitoids. In many cases, if it is unresolved among adult females on a patch of hosts, extrinsic competition may lead to intrinsic competition among their developing offspring. Furthermore, as explored below, extrinsic competition may counter the effects of intrinsic competition.

In this review, we describe different types of extrinsic competition among male and female parasitoid wasps occurring along a continuum that includes host habitat and food plant location, host and mate finding, parasitism, and brood attending behavior. We show that life history, host use, and reproductive strategies are strongly correlated with different types of extrinsic competition. Most importantly, patterns of reproductive investment (including patch time allocation, niche segregation, and physical aggression) determine how extrinsic competition is manifested. We then explore the population- and community-level consequences of extrinsic competition, including phenomena such as competitive displacement and apparent competition. Finally, we consider how anthropogenic factors such as habitat fragmentation, pesticide use, and climate change might be expected to alter the outcomes of extrinsic competition and the effects on the structure of communities involving parasitoids. Our synthesis complements a previous review in this journal (81) that examined intrinsic competition in hymenopterous parasitoids, focusing on strategies employed by parasitoid larvae to monopolize host resources.

INTERFERENCE AND EXPLOITATIVE COMPETITION

Competition, whether among females for hosts or among males for mates, is generally categorized as either interference or exploitative. Interference competition occurs when competing individuals

f Competitive displacement

Aphytis melinus

Aphytis lingnanensis

Aonidiella aurantii

g Apparent competition

Gelis agilis

Cotesia glomerata

Cotesia melitaearum

Pieris brassicae

Melitaea cinxia

♀

♂

c

d

e

a

b

Figure 1

(*a*) Intrinsic competition between immature *Cotesia glomerata* larvae (*left*) and *Cotesia rubecula* larva (*right*). The *C. rubecula* larva possesses enlarged mandibles with which it kills the larvae of *C. glomerata* (*center*). As such, this is an example of intrinsic, interspecific, interference competition. (*b*) Intrinsic, intraspecific competition between larvae from two *C. glomerata* broods produced by different females (outlined in *black* and *blue*, respectively). As *C. glomerata* is a gregarious species, its larvae do not engage in aggressive attacks over host resources; instead, they engage in exploitative competition (for a full review of intrinsic competition, see 81). (*c–e*) Extrinsic competition, i.e., competition between adults. (*c*) Male–male competition for mates. Two males (without ovipositors) fight for access to females (with ovipositors; shown above the males). Depending on the species, males may aggregate at the female's site of emergence or oviposition, where they may engage in either interference competition (e.g., physical attack) or exploitative competition. Male behaviors can be broadly categorized as being precopulatory and postcopulatory. Male–male competition is exclusively intraspecific. (*d*) Intraspecific female–female competition for hosts. Intraspecific competition may be interference or exploitative (e.g., see panels *a* and *b*). (*e*) Interspecific female–female competition may also be interference or exploitative. Differences in morphology (e.g., ovipositor length, size), foraging efficiency, or spatial and temporal segregation in foraging behaviors may determine the winner of competitive interactions. (*f*) Competitive displacement occurs when two consumers use the same resource, and one consumer is able to persist at a lower resource density than the other, thereby displacing the second consumer. In a well-studied example, *Aphytis melinus* is able to displace *Aphytis lingnanensis* because it attacks younger host instars of the California red scale (*Aonidiella aurantii*) and is able to forage more efficiently at warmer temperatures. (*g*) Apparent competition is the indirect negative interaction between two species that share one or more natural enemies but do not directly compete for the same host resource. In this example, the addition of *C. glomerata* to a hyperparasitoid (*Gelis agilis*)–parasitoid (*Cotesia melitaearum*)–host (Glanville fritillary, *Melitaea cinxia*) system results in an increase in the *G. agilis* population, with dire consequences for *C. melitaearum* (*orange arrow*).

directly interact, preventing one another from accessing needed resources (**Figure 1*a***). Exploitation competition occurs when some individuals are more efficient at locating and using limiting resources than are other individuals (**Figure 1*b***). Competing individuals in this case do not directly interact. Interference competition, in contrast, can be intense even if the level of the resource is not limiting. These categories are not necessarily mutually exclusive, as many examples likely include

aspects of both interference and exploitation. Many of the mechanisms involved in interference and exploitative competition among individuals also underlie population- and community-level phenomena such as apparent competition and competitive displacement.

FEMALE–FEMALE COMPETITION FOR HOSTS

Life-History Strategies and Extrinsic Competition in Females

Parasitoid wasps are a phylogenetically diverse group of organisms (64) and exhibit several dichotomous strategies in locating and exploiting host resources. These strategies are often correlated and affect the intensity and outcome of extrinsic competition among adult females.

Two types of parasitoids, koinobionts and idiobionts, have been described based on differing physiological interrelationships with their hosts. Koinobionts are parasitoids that develop in hosts that continue feeding and growing after parasitism. The vast majority of koinobionts are endoparasitoids that lay tiny, yolkless eggs inside their hosts, where larvae feed and develop; such eggs are termed hydropic because they must absorb host hemolymph proteins to complete embryogenesis (80, 97). Idiobionts are parasitoids that attack nonfeeding host stages (eggs, pupae) or hosts that are paralyzed before oviposition (11, 184). Many idiobionts that parasitize late-instar hosts (i.e., larvae or pupae) are ectoparasitic, and the neonate parasitoid larva(e) pierce through the host cuticle with their mandibles and feed externally throughout their larval development. Such species lay relatively large, yolk-filled anhydropic eggs that contain all the resources necessary to complete embryogenesis (97).

Such differences between koinobionts and idiobionts in terms of investment per egg have two important consequences for extrinsic competition. First, because anhydropic eggs are costly to produce and store, many (though not all) idiobiont ectoparasitoid adult females must obtain supplementary host proteins to mature additional eggs through host-feeding, whereby the adult female punctures the host cuticle with her ovipositor and then drinks the host hemolymph that oozes from the wound. Host-feeding is typically necessary to mature additional eggs as well as to increase the lifespan of the feeding adult. Furthermore, host-feeding often kills the host, along with any offspring laid by a competing female. Importantly, host-feeding does not occur in koinobiont endoparasitoids (97). Second, idiobiont parasitoids producing costly anhydropic eggs exhibit competitive behaviors such as brood guarding and fighting that are virtually absent in koinobiont species.

Interference Competition: Brood Guarding and Fighting

Parasitoid adult females often use aggressive behavioral strategies to monopolize hosts where hosts are aggregated on patches or, alternatively, on patches where hosts are scarce. For instance, some female parasitoids may guard host patches by aggressively chasing other females away or, when this fails, through physical combat. Brood guarding and fighting behaviors have been demonstrated in several idiobiont species (13, 60, 79, 92, 127, 131, 132). Among the best-described examples of brood guarding and fighting are larval parasitoids in the family Bethylidae and egg parasitoids in the families Mymaridae and Scelionidae. Females in these families frequently guard parasitized hosts until their progeny have hatched. Mothers will even attack and kill other females that attempt to super- or multiparasitize hosts (13, 70, 73, 79, 89, 131, 132, 152) (**Figure 2a**). This phenomenon has also been observed in hyperparasitoids, such as the solitary secondary cocoon hyperparasitoid *Trichomalopsis apantelocetena*, where females will defend entire cocoon clusters (containing 30 or more cocoons) of their gregarious host *Cotesia kariyai* for up to several days from other females with behaviors that include biting, physical displacement, and ovipositor jabbing (127) (**Figure 2b**).

Figure 2

(*a*) Host and brood guarding by the gregarious idiobiont ectoparasitoid *Goniozus legneri* Gordh (Hymenoptera: Bethylidae). In this case, two females are involved in antagonistic interactions for control of a paralyzed host caterpillar of *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae). (*Left*) After paralyzing the caterpillar, one female bites at the abdomen of a second female in an attempt to displace her from the host. (*Right*) A parasitoid female aggressively guards both the paralyzed host caterpillar and her 11 eggs on the surface of the paralyzed host. Photos courtesy of Sonia Dourlot (see **http://www.soniadourlot.com/**). (*b*) Two females of the gregarious idiobiont ectohyperparasitoid *Trichomalopsis apanteloctena* Crawford (Hymenoptera: Chelonidae) fighting for control of cocoons of their primary parasitoid host, *Cotesia kariyai* Watanabe (Hymenoptera: Braconidae). In these encounters, one female is occasionally killed by the other. Photo courtesy of Toshiharu Tanaka.

It may take up to several days for an individual female hyperparasitoid to parasitize most of the cocoons, explaining the extended period of guarding.

Several interacting context- and trait-dependent factors determine whether it is evolutionarily adaptive for females to defend individual hosts (before or after parasitism) and host patches. Metabolic resource investment per egg by female parasitoids is critically important. Prolonged brood guarding and fighting (potentially leading to the death of the loser) are almost exclusively restricted to ectoparasitic idiobionts. Many idiobionts attack scarce or concealed late-larval or pupal hosts, where the overproduction of eggs would have little adaptive benefit (96, 97). These parasitoids invest much more resources per capita in the production of small numbers of large, anhydropic eggs than koinobionts do in the production of large numbers of small, hydropic eggs (95, 97, 139). Furthermore, host handling times for idiobionts are generally much longer than those of koinobionts (97). For example, the ectohyperparasitoid *Gelis agilis*, which can lay no more than 2–3 anhydropic eggs per day, sometimes takes up to several hours to lay a single egg into the cocoon of its primary parasitoid host (79). By contrast, many koinobionts can lay eggs in a fraction of a second (80). For koinobionts, there is little utility in wasting time guarding individual hosts when time would be optimally better spent searching for other hosts.

Brood guarding and fighting in parasitoids are tightly linked with two parameters, resource value (RV) and resource holding potential (RHP). Both parameters function asymmetrically and are driven by a range of biotic and abiotic factors, such as competition and temperature (102). RV is also determined by host quality and abundance, as well as by parasitoid biology and ecology. Hosts attacked by egg-limited idiobionts represent a valuable resource, especially when handling times (times necessary for paralyzing and parasitizing hosts) are extended. Large hosts or host clusters, where a female can produce large or many offspring, respectively, are also of high intrinsic value. RHP describes the ability of an individual female parasitoid to defend and monopolize hosts. The intensity and eventual resolution of conflicts between parasitoid females may hinge on the value of the resource and on traits, such as body size and physiological condition, of the combatants. For instance, larger females are often able to displace smaller females from hosts, irrespective of the larger females' owner-intruder status and RV (73). The importance of other traits, such as

Hydropic eggs: eggs that are small and typically yolkless and must absorb nutrients from the host hemolymph; typically produced by koinobiont species

parasitoid age, health, or egg load, on the outcome of aggressive interactions has to date been little studied.

Extrinsic competition and aggression among female parasitoids may generate outcomes where the owner (first arrived) female wins or where she is driven off or killed by the intruder. In the latter case, competition is often resolved through lethal interference. In this instance, female parasitoids monopolize or kill hosts that have been previously parasitized by con- or heterospecific females. This can be done in two distinctly different ways. In the first, parasitoid females insert their ovipositors either directly into previously laid eggs (in the case of ectoparasitoids) or into previously parasitized hosts to kill eggs or larvae inside of them, a process known as ovicide or larvicide (93, 106, 131, 159, 163). In the second mechanism, female parasitoids destructively host-feed on previously parasitized hosts, killing the eggs and larvae of the previous female in the process (35, 90, 201). Host-feeding behavior is primarily restricted to parasitoids producing anhydropic eggs and is another trait that is often correlated with brood-guarding behavior.

While largely restricted to idiobiont parasitoids that have long host handling times, host-guarding behavior has been observed in females of the solitary koinobiont endoparasitoid *Venturia canescens*, which tussle and jab their ovipositors at other females when foraging for their caterpillar hosts (*Plodia interpunctella*) on the same patch (172). Although antagonistic encounters like this are probably commonplace among many species of koinobiont parasitoids that attack numerous, highly aggregated hosts, they are rarely protracted or lethal. This is because host handling times in koinobionts are generally very short (e.g., <1 s), and it is therefore a better strategy to parasitize as many available hosts as possible (139). In this context, fighting behavior among koinobionts may be aimed at displacing other females from host patches, allowing dominant females to monopolize them. More generally, koinobionts may nevertheless engage in more diffuse forms of exploitative extrinsic competition. The vast majority of koinobiont parasitoids are time limited and will therefore die long before they have exhausted their full potential complement of eggs. Given that hosts are distributed discretely in patches, parasitoid fitness depends on optimal allocation of time to host finding and exploitation.

Extrinsic Competition and Patch Time Allocation in Females

Optimal foraging models assume that parasitoid females should forage in such a way as to maximize their encounter rate with unparasitized hosts (36, 176, 191). The ratio of unparasitized to parasitized hosts in patches will be reduced to a critical value at which it is adaptive for female parasitoids to leave the patch to search for more profitable patches elsewhere (191); however, there are caveats to this rule (see below). Many of these models have been tested with koinobiont endoparasitoids that produce copious numbers of small hydropic eggs early in adult life that can be injected rapidly into their hosts (120). Given that koinobionts can generally parasitize many individual hosts in a small period of time, when parasitoid densities are high, host patches can be rapidly depleted of unparasitized hosts, resulting in an ever-increasing risk of females re-encountering previously parasitized hosts. This problem is amplified as parasitoid density increases. Under these conditions, koinobiont parasitoids face two choices: (*a*) whether to remain on a patch where the encounter rate of unparasitized hosts is steadily declining or leave in search of higher-quality patches elsewhere, and, if they stay, (*b*) whether to accept (i.e., engage in superparasitism or multiparasitism leading to intrinsic competition) or reject previously parasitized hosts. These foraging options are based on a complex interplay of ecological (e.g., host density and spatial distribution) and physiological and behavioral (e.g., female age, egg load, handling time, physical condition, previous experience) parameters. These parameters have been captured by a range of optimal foraging models, including the marginal value theorem (142), and by dynamic optimization models (113).

Numerous studies have shown that parasitoids balance their foraging and patch residency decisions based on the depletion rate of healthy hosts and the number of competitors present (for reviews, see 120, 176, 191). One shortcoming of optimal foraging models is that they generally assume that competitors are equal. However, several studies report that smaller or competitively inferior parasitoids are more likely to leave host patches earlier than predicted in optimal foraging models when they are confronted by more aggressive intra- or interspecific competitors (59, 69, 91, 193). Aggression may in turn be a species- or individual-specific trait, or it may vary with the age, egg load, and physiological condition of the parasitoids foraging within a patch (192). Optimization models show that parasitoid oviposition decisions (such as clutch size) are influenced by internal (state) variables (145). These models, however, have been little studied in the context of extrinsic competition.

Ideal Free Distribution Under Extrinsic Competition

Most koinobionts are highly specialized and will only attack one or a few species of herbivore hosts in nature (67). Given the clustered distribution of herbivores and their food plants, competition for hosts among parasitoids is likely to be intense under certain conditions, such as when hosts are scarce or when travel times to neighboring host patches are high (176). Once on a patch, female parasitoids may mark parasitized hosts or even host patches with marking (also known as epideictic) pheromones that convey the status of the patch to other females (85, 144). When several parasitoid females simultaneously exploit the same host patch in habitats where nearby host patches occur, they are expected to distribute themselves optimally among different patches. As parasitoid densities increase, or as host numbers decrease, antagonistic encounters are expected to increase both interference and exploitative competition and subsequent changes in the dynamics of patch residency by parasitoids.

Ideal free distribution (IFD) models broadly predict that female parasitoids should distribute themselves within and between patches in ways that ensure that the encounter rate of unparasitized hosts is more or less equal among them (57, 119, 171). Interference competition IFD models include several other predictions based on the presence of competitors (121, 160, 170). The most important prediction is that the ratio of individuals foraging in different patches matches the ratio of resources in these patches. To date, despite extensive early modeling, surprisingly few empirical studies have examined IFD in parasitoids, and these provide only limited support for most IFD predictions (166, 172, 198, 199). For example, Tregenza and colleagues (172) found that only some predictions of IFD models under interference competition were upheld in the solitary koinobiont *V. canescens*. Another study used parentage analysis on microsatellite genotypes to test IFD in a natural population of the aphid parasitoid *Lysiphlebus testaceipes* (166), finding that the number of progeny per parasitoid foundress was not correlated with the number of aphid hosts per colony (in support of IFD predictions). However, in contrast with IFD predictions, offspring number was affected by the number of foundresses (166). A study of a tephritid fly, *Terellia ruficauda*, and its parasitoid complex (two species of *Pteromalus* and two species of *Torymus*) found little evidence to support IFD model predictions—that herbivore and parasitoid densities should both be positively correlated with resource density. Instead, both the fly and the parasitoids preferentially foraged and oviposited on isolated thistle plants (*Cirsium palustre*), which the authors of the study attributed to reduced risk of mammalian herbivory, which is more prevalent in denser stands of thistle (199).

The paucity of studies to date hinders our understanding of how extrinsic competition affects the distribution of parasitoids on patches under potential interference competition. One major shortcoming of previous models is that none, as far as we know, have incorporated important physiological factors of female parasitoids, like egg load, age, and physiological condition, that

may clearly affect foraging behavior and decision-making processes (145). These factors are virtually impossible to determine in the field and are often strictly controlled in laboratory experiments. Moreover, abiotic conditions in nature are highly variable both spatially and temporally, and weather conditions, for example, may strongly affect parasitoid foraging behavior and influence competition (196).

Exploitative Competition

While theory broadly predicts that overlapping resource requirements among multiple species hinders coexistence (44), adult parasitoids use several strategies to partition shared hosts, including divergence in morphological and behavioral functional traits, dividing foraging activity along spatial and temporal scales, and exploiting competitor-free spaces (8, 32, 153).

Morphological traits mediating competition: ovipositor length. For hosts that are concealed within substrates (e.g., wood, fruit), variation in parasitoid ovipositor length can reduce the intensity of interspecific competition for hosts occurring at different depths (71, 72). Three species of *Megarhyssa* (Ichneumonidae) coexist because differences in their ovipositor lengths permit access to larvae of their pigeon horntail hosts (*Tremex columba*) feeding at different depths within the trunks of dead and dying hardwood trees (66, 82). Similarly, of the braconid parasitoids of tephritid fruit flies in Mexico, *Utetes anastraphae* larvae outcompete *Doryctobracon areolatus* larvae when both parasitize the same host, but the longer ovipositor of adult *D. areolatus* enables it to find hosts buried deeper in large fruit that are inaccessible to adult *U. anastraphae*, which has a shorter ovipositor (6).

Behavioral traits mediating competition: foraging efficiency. Adult parasitoids with more efficient foraging behaviors are expected to be stronger extrinsic competitors. Foraging efficiency is determined by the time spent locating hosts (search time), the duration of the oviposition sequence (handling time), and the quality of hosts accepted (67, 80). When intrinsic competition favors the first parasitoid that attacks a host (81, 195), species with slow search times have reduced foraging efficiency and risk being displaced by faster competitors (78). Extrinsic competition can counter the effects of intrinsic competition (33, 38, 63, 141). An interesting example of this comes from a study of competitive displacement of a native parasitoid, *Praon pequodorum* (Braconidae), by *Aphidius ervi*, another braconid parasitoid introduced to *P. pequodorum*'s home range to control the pea aphid. Both species are solitary endoparasitoids. Interestingly, *P. pequodorum* is thought to be a superior intrinsic competitor due in part to a protective extraserosal envelope surrounding developing embryos that protects them from physical attack by *A. ervi* larvae (40). Nevertheless, *A. ervi* adults exhibit more efficient foraging behaviors (and are superior extrinsic competitors) than *P. pequodorum* adults, allowing *A. ervi* to largely exclude *P. pequodorum* in most regions where the two species co-occur (149).

Search time is correlated with a parasitoid's ability to use host-associated infochemicals (e.g., kairomones, synomones), with faster search times being associated with higher sensitivity to cues indicative of host presence (34, 42, 136). Superior host-finding abilities can also arise from a parasitoid's ability to use a greater diversity of host-related cues (39). *Trissolcus basalis* and *Ooencyrtus telenomicida* both compete for *Nezara viridula* eggs, but *T. basalis* locates hosts more quickly because it exploits a wider range of volatiles associated with *N. viridula* oviposition and mating behavior, whereas *O. telenomicida* uses only cues associated with the host's virgin males (135, 136). Furthermore, associative learning of chemical cues is a significant element of parasitoid foraging behavior that can determine the outcome of competitive interactions among adults (39). For example, foraging female *V. canescens* can learn to associate novel odors with parasitized hosts and

conspecific females and subsequently avoid these odors when foraging for unparasitized hosts (57). This suggests that learning helps *V. canescens* to avoid costly intraspecific competition.

Handling time is often positively correlated with the number of eggs laid per attack, with solitary parasitoids generally having faster oviposition times than gregarious parasitoids (185). Faster handling times increase the number of hosts that can be attacked per unit of time (140), as well as decreasing a female's risk of predation (12). The presence of interspecific competitors can alter handling time. Populations of the figitid *Leptopilina heterotoma* that compete with *Leptopilina boulardi* for *Drosophila melanogaster* larvae have faster handling times than populations of *L. heterotoma* that do not experience interspecific competition (133). Oviposition behavior and host defenses can interact to indirectly favor specific foraging strategies among competing parasitoids. Whereas oviposition by *Aphidius picipes* does not elicit strong defensive reactions from the English grain aphid *Sitobion avenae*, attacks by *Aphidius rhopalosiphi* increase defense responses, causing *A. rhopalosiphi* to leave patches with remaining unparasitized hosts that are then available to *A. picipes* (177).

Adult foraging efficiency is enhanced when parasitoids avoid superparasitism or multiparasitism by detecting host quality cues indicative of previously parasitized hosts. Such discrimination may occur in flight (58, 164, 202); while antennating potential hosts, which often includes detecting marking pheromones deposited by previous females (107, 128); or during oviposition (30, 179). The population history of contact with competitors may also affect the avoidance of previously parasitized hosts. *Cotesia glomerata* and *Cotesia rubecula* both attack the cabbage white *Pieris rapae* throughout North America. In regions where the two co-occur, *C. glomerata* exhibits much stronger avoidance behaviors of hosts previously attacked by *C. rubecula*, compared to behavior in regions where only *C. glomerata* is present (187).

Behavioral traits mediating competition: temporal and spatial segregation. Competing adult parasitoids can diffuse competition by partitioning host resources in time and space (7, 9, 75), and many species alter their foraging niches in the presence of heterospecific competitors (see 81 and references therein). Differential performance of competing parasitoid species across temperature gradients may result in coexistence or displacement, depending on whether temperature variation is temporal or spatial. Classic studies on temperature-mediated effects on foraging behavior and competition among three *Aphytis* (Aphelinidae) species that attack California red scale *Aonidiella aurantii* represent excellent examples of this. In areas such as eastern Spain, coexistence is mediated by temporal niche partitioning, with the native *Aphytis chrysomphali* being more abundant in late winter and early spring and *Aphytis melinus* becoming dominant in the hotter, drier summer months (156). In southern California, geographical differences in temperature appear to determine which *Aphytis* species outcompetes the others. *Aphytis melinus* forages more efficiently and survives higher temperatures in the hotter, drier inland valleys, where it has displaced *Aphytis lingnanensis* (46). *Aphytis chrysomphali* and *A. lingnanensis* predominate in the cooler, coastal valleys (45).

Adult parasitoids can also reduce extrinsic competition by shifting or constricting their niche space through plant-mediated host-partitioning segregation at smaller spatial scales (200). *Encarsia pergandiella* restricts its foraging activity along the vertical axis of cotton plants in the presence of *Eretmocerus mundus*, which outcompetes *Eretmocerus pergandiella* for silverleaf whitefly (*Bemisia argentifolii*) hosts (17). *Aphytis melinus* and *Encarsia perniciosi* both parasitize California red scale on citrus tree leaves and stems, and while *A. melinus* invariably outcompetes *E. perniciosi* when both attack the same host individual, adult *A. melinus* prefer foraging for the larger hosts found on leaves instead of the smaller hosts found on stems (21, 194).

Behavioral traits moderating competition: host preference shifts. Adult parasitoids can minimize or eliminate competition by foraging for alternative hosts in the presence of stronger

competitors. In Hawaii, despite being a weaker intrinsic competitor, *Diachasmimorpha tryoni* persists by shifting its foraging on lantana plants, where it parasitizes a novel host species, the lantana gall fly, *Eutreta xanthochaeta* (Aldrich), a dipteran ignored by the superior competitor *Fopius arisanus*; interestingly, the gall fly enhances *D. tryoni* survival only when *F. arisanus* is present (118).

Parasitoids can reduce competition by attacking hosts at different ontogenetic stages. Even though host size is often positively correlated with adult parasitoid size and fitness (186), parasitoids can mitigate competition by attacking smaller hosts (23). Studies on the California red scale and its *Aphytis* spp. parasitoids provide some of the best field-based evidence of how host size preferences affect extrinsic competition and competitive displacement (46, 125) (**Figure 1f**). In California, a preference for smaller hosts allows *A. melinus* to displace *A. lingnanensis* by reducing the number of hosts that grow large enough for *A. lingnanensis* to produce female progeny (109). Similarly, displacement of *A. chrysomphali* by *A. melinus* has been observed in many parts of the Mediterranean basin, with *A. melinus* tending to lay more eggs and accepting more heterospecifically parasitized hosts than does *A. chrysomphali* (26, 27). In Spain, *A. chrysomphali* avoids displacement by shifting its host-size preferences depending on activity of the dominant *A. melinus* (129, 130). Use of younger host instars does not always result in a competitive advantage. The black (olive) scale *Saissetia oleae* is attacked by *Metaphycus* spp. parasitoids and *Coccophagus lycimnia*. *Metaphycus* spp. readily attack younger scale hosts, whereas *C. lycimnia* require older hosts in which to produce daughters. Despite the apparent advantage of *Metaphycus* spp., *C. lycimnia*, as an autoparasitoid, hyperparasitizes *Metaphycus* larval females to produce their own males (114).

MALE–MALE COMPETITION FOR MATES

As is the case for competition between adult female parasitoids for hosts, the nature of competition between male parasitoids for access to mates depends strongly on the spatial and temporal distribution of adult females in the environment, as well as the specifics of female reproductive biology (22, 56) (**Figure 1c**). Unlike competition between adult females for hosts (often to avoid multiparasitism), competition between males for access to females is almost entirely restricted to intraspecific competition, and most studies focus on interference competition. Males often aggregate at sites where females can be reliably found—i.e., at sites where females emerge as adults or at oviposition sites. In the case of the former, many species are protandrous, i.e., males develop faster and emerge before females from a host or group of hosts. In many of these situations, males and females are brothers and sisters (if they are offspring from a single mother). In these cases, the optimal sex ratio is predicted to be female biased, as this will reduce the competition between brothers for mates (76, 77). As more females (foundresses) contribute offspring to a patch, predicted sex ratios approach equality, and the competition among (unrelated) males for mates increases. This phenomenon, known as local mate competition, has a rich history of theory, experimentation, and review (e.g., 28, 67, 197) and is not considered further in this article. Features such as the tendency to remate (ranging from never to always), the degree of sperm precedence, and the location of mating sites (e.g., at the site of adult emergence, at the site of oviposition, in mating swarms) all determine the likelihood and intensity of male–male competition for mates. Male–male competition can be particularly intense in species where the remating frequency of females is low or sperm precedence is high. Both precopulatory and postcopulatory courtship behaviors by males can alter the likelihood of remating.

Precopulatory Male–Male Competition

Precopulatory behaviors include territorial displays and male–male aggression. In many protandrous species, early emerging males remain near their natal host, often defending territories,

waiting to mate with females (often their sisters) as they emerge (101, 161) or even before they emerge (for *Trichogramma dendrolimi*, see 161; for *Nasonia giraulti*, see 50, 104; for *Laelius pedatus*, see 117). Early emerging males of several scelionid egg parasitoids attack later-emerging males, dominating mating opportunities within a host patch (189). Male territoriality in many of these species begins to transition to scramble competition as the number of males present increases and defense of mating sites becomes more difficult (55). Fighting between males of some species of the eulophid genus *Melittobia* can have more severe consequences, with death as the outcome for the loser (3, 4, 180). Larger males win fights in some species (e.g., 111), but size has little effect on the outcome of male–male contests in other species (e.g., 31). Males of other parasitoid species are known to disperse in search of locations where females are about to emerge and guard these sites against other intruding males (for rhyssine ichneumonids, see 52, 53; for *Nasonia* spp., see 104, 112; for *C. glomerata*, see 162) or patches of hosts to be visited by ovipositing females (e.g., *Trichogramma*; see 101, 161). Short-range sex pheromones are likely important in many parasitoid species (180), but there are few documented cases of long-range sex pheromones (54, 67). In the case of *Lariophagus distinguendus* (Pteromalidae), a parasitoid of stored grain insects, male pupae mimic female pupae in that both produce sex pheromones attractive to males that have already emerged (158). Presumably, distraction by this chemical mimicry increases the likelihood of mating for the later-emerging males.

One of the best-studied systems of precopulatory male competition involves three closely related species in the genus *Nasonia* (Pteromalidae), gregarious ectoparasitoids of flesh fly and blow fly pupae in the genera *Calliphora*, *Protocalliphora*, and *Sarcophaga* (41). In some species, males are wingless or are brachypterous (and flightless); consequently, males in these species must mate with females as they emerge from their hosts. In the case of the flightless *Nasonia vitripennis*, males eclose before females (i.e., are protandrous) and chew holes in the puparia of their hosts through which they emerge and establish territories. Males are aggressive in their defense of space around the host so that they can mate with females as they emerge. In contrast, *N. giraulti* females are receptive to mating before emerging from their host puparia, and males mate with females (sisters) within the host before emergence (50, 104). Correspondingly, sex ratios of *N. giraulti* are more female biased than those of *N. vitripennis*, reflective of the more intense local mate competition conditions experienced by the former (50). Within-host mating in *N. giraulti* has been suggested to be a mechanism that reduces hybridization with *N. vitripennis* (50). *Nasonia vitripennis* males exhibit territoriality, whereas *N. giraulti* males do not (104, 112)—both male size and prior experience with the territory provide advantages to males in winning contests. Territoriality and aggressive behaviors generally include pursuit of one male by another, charging or lunging, and kicking (104). *Nasonia longicornis* shows intermediate levels of within-host mating and male–male aggression (104).

Postcopulatory Male–Male Competition

Little is known about male postcopulatory behaviors in parasitoids, although where they have been documented, they can be very effective in preventing subsequent matings. Mate guarding reduces the likelihood that recently mated females remate with a subsequent male. Such behaviors are particularly important when the likelihood of finding additional mates is low or in species with last-male sperm precedence. Mate guarding by male *A. melinus* significantly reduces the likelihood that a second male is able to sire any offspring; however, if the first male is removed before mate guarding occurs, then the proportion of offspring sired by a second male doubles (5). Similarly, postcopulatory male behaviors make female *Spalangia endius* (Pteromalidae) less attractive and receptive to subsequent males (100). *Nasonia giraulti* males exhibited longer postcopulatory displays

than either *N. vitripennis* or *N. longicornis* males, and, correspondingly, female *N. giraulti* were less likely to remate within the first 10 minutes (105). These species differences in postcopulatory displays and remating frequencies reflect differences in where females mate; in *N. giraulti*, almost all mating occurs in the host puparium, whereas in *N. vitripennis*, females are receptive only after emerging from the host, and both males and females likely have mating opportunities as females leave the surface of the host puparium but before they disperse from the natal patch (105). Finally, after mating, male *C. rubecula* have been shown to mimic female behaviors to distract other rival males, a phenomenon that has been described as a form of postcopulatory mate guarding (61).

POPULATION- AND COMMUNITY-LEVEL CONSEQUENCES OF EXTRINSIC COMPETITION

Many of the morphological, physiological, and behavioral mechanisms responsible for extrinsic competition at an individual level (discussed above) result in population- and community-level patterns involved in competitive displacement and apparent competition (e.g., 83). Competitive exclusion and apparent competition are conceptually and theoretically related in that pairs of species within a trophic level may indirectly interact via a third species in an adjacent trophic level (86–88, 150).

Competitive Displacement and Exclusion

Competitive displacement (exclusion), where an invading species drives a previously established species locally extinct, is the most extreme outcome of interspecific competition. Some of the most compelling examples of competitive displacement among insects are found in biological control programs (44, 143). A classic example of competitive displacement among parasitoids involves three species of *Aphytis* that attack the California red scale, *A. aurantii* (**Figure 1f**). *Aphytis chrysomphali* was presumably accidentally introduced along with its host, *A. aurantii*, into southern California, where it was widespread until the introduction of *A. lingnanensis* in 1948 (46). Introduction of *A. melinus* in the mid-1950s quickly led to the competitive displacement of *A. lingnanensis* in the hotter, drier inland valleys (46). As discussed above (see the section titled Behavioral Traits Mediating Competition: Host Preference Shifts), differences in the ability to forage in hotter climates and the ability to successfully develop on younger, smaller hosts have enabled *A. melinus* to displace *A. chrysomphali* and *A. lingnanensis* in different citrus-growing regions of the world. Similarly, differences in foraging efficiency and the ability to use younger, smaller cassava mealybug (*Phenacoccus manihoti*) hosts also explain the ability of the encyrtid *Epidinocarsis lopezi* to competitively exclude *Epidinocarsis diversicornis* in central and southern Africa (74, 137). That these two species of *Epidinocarsis* coexist in their native South America is in part due to the availability of alternative hosts for *E. diversicornis*, which are not present in Africa (138). *Pieris rapae* (known as the imported cabbage worm in North America) and its two parasitoids, *C. glomerata* and *C. rubecula*, represent another well-studied example of competitive displacement. *Cotesia rubecula* has displaced *C. glomerata* throughout much, but not all, of its former range in North America (84). Whether displacement occurs likely depends on a mix of intrinsic factors, such as physical and physiological suppression among larvae, and extrinsic factors, such as differences in foraging efficiency (134, 186) or susceptibility to hyperparasitism (188). In Western Europe, where this system originates, these two parasitoids coexist in the same location largely because they use different host species. *Cotesia rubecula* exclusively attacks *P. rapae*, whereas *C. glomerata* predominately attacks the large white, *Pieris brassicae* (65), a host that does not occur in North America.

In each of these cases, the superior competitor is thought to be able to persist on lower densities of their hosts, and it is this ability that drives displacement (124, 126). More generally, the dominant

competitor should be the one that suppresses resource levels to below that required to support a competitor's population while still being able to persist itself (168).

Apparent Competition in Parasitoids

Apparent competition is the indirect negative interaction between two species that share one or more natural enemies, even if they do not share the same resource. For instance, if one parasitoid population increases the carrying capacity of the consumer population (e.g., predator or hyperparasitoid), then the consumer population could significantly depress, or even drive to extinction, a second parasitoid population if the latter is the preferred resource (99) (**Figure 1g**). Predators and hyperparasitoids can differentially shift the foraging behaviors and efficiencies of parasitoid females as they search for hosts to parasitize via both consumptive (including intraguild predation) and nonconsumptive effects (e.g., 37, 62, 148, 155).

Host–parasitoid interactions have proven to be valuable systems for theory development, as well as for empirical tests with which to demonstrate the importance of apparent competition and enemy-free space (18–20, 99). The majority of empirical examples of apparent competition involving parasitoids are cases where the parasitoid is the natural enemy (20, 88, 99). However, examples exist of apparent competition between two primary parasitoids effected by hyperparasitoids (e.g., 122, 182). This is well exemplified in a study where *C. glomerata* was experimentally introduced to a natural system involving the Glanville fritillary *Melitaea cinxia*, its specialist parasitoid *Cotesia melitaearum*, and the generalist hyperparasitoid *G. agilis*. As *C. glomerata* was an additional host for *G. agilis*, its introduction resulted in an increase in the population of the hyperparasitoid and a concomitant decline in *C. melitaearum*, even though the two *Cotesia* species attack different caterpillar species (182) (**Figure 1g**). In general, the resource species that persists (or thrives relative to the other) is the one that supports (and persists under) the higher consumer population density (88).

The existence of apparent competition is more difficult to detect when it is concurrent with direct competition. The *C. glomerata–C. rubecula–P. rapae* system described above represents such a variation on apparent competition. In some North American populations, both *Cotesia* species engage in direct, exploitative competition, as they both attack *P. rapae* caterpillars and are sometimes found attacking the same host individual (187). Coexistence of these species may be facilitated by the differential impacts of hyperparasitoids. While both *C. rubecula* and *C. glomerata* broods were equally likely to be attacked by hyperparasitoids (shared by both *Cotesia* species), the resulting within-brood mortality from such attacks was 100% for the solitary *C. rubecula*, whereas a significant fraction of the *C. glomerata* cocoons within a brood always escaped hyperparasitism. Furthermore, individual *C. rubecula* cocoons are larger than *C. glomerata* cocoons, resulting in the preference of hyperparasitoids for *C. rubecula* (188). Taken together, these effects suggest that apparent competition helps to counter the effects of competitive displacement, thereby allowing the coexistence of the weaker direct competitor *C. glomerata* with the stronger competitor *C. rubecula* (188).

EXTRINSIC COMPETITION IN A CHANGING WORLD

Biodiversity is under threat from a range of anthropogenic stresses (49). These threats include habitat loss and fragmentation; invasive plants and animals; various forms of pollution, including chemical pesticides and fertilizers; and climate change (48). Recent evidence suggests that many insect groups are declining rapidly across different parts of the biosphere (146, 147, 190). One of the biggest consequences of declining insect populations is the effect that it will have on multitrophic interactions and food webs and, in turn, on ecosystem functioning (181). Evidence suggests that food webs are more prone to breaking down when highly connected species are removed from them (51). The structure and stability of parasitoid–host food webs are likely sensitive to land use

intensification, biotic invasions (of both plants and insects), environmental toxins (especially in the form of insecticides, herbicides, and fertilizers), and climate change (174).

As we show above, extrinsic competition in its many forms plays a major role in the structure and functioning of herbivore–parasitoid communities. However, human-mediated changes and/or simplification of habitats and plant patches are likely to alter the dynamics of these competitive interactions in diverse ways. In some instances, they may intensify competition among parasitoids by reducing impediments to host finding. For example, in cropping systems, plants are generally grown in simple monocultures that enhance the ability both of herbivores to find their food plants and of specialized natural enemies like parasitoids to find their hosts (2). Because many parasitoids use herbivore-induced plant volatiles (HIPVs) to locate their hosts (173), a reduction in the chemical or structural heterogeneity of a patch, such as in fragmented habitats, can significantly affect parasitoids' host-finding ability (68). This may alter the strength of competitive hierarchies among parasitoids sharing the same host, leading to competitive exclusion of the inferior species. In contrast, invasive plants, whose introduction is often the direct result of global trade, are well known to alter the community structure in which parasitoids forage (16). While little is known about how parasitoid foraging responds to changes to HIPVs at larger, landscape scales (1), changes to plant community structure and HIPV complexity likely alter the foraging efficiency of and decisions made by parasitoids. As discussed above, such effects on foraging efficiency will alter the outcome of extrinsic competition among parasitoids and, ultimately, affect parasitoid community structure. Similarly, the introduction of additional herbivore species can differentially reduce the foraging efficiency of potentially competing parasitoid species (43) and hyperparasitoid species (165).

Changes in mean temperature, as well as in the frequency of extreme temperature events, resulting from climate change have dramatic effects on species interactions and trophic networks, including host–parasitoid food webs (167, 175). Increases in temperature likely result in phenological mismatches between interacting species, as well as in range expansions (both poleward and toward higher elevations) (25, 110, 151). Such mismatches resulting from climate change not only have the potential to affect direct trophic interactions, such as host–parasitoid and plant–herbivore interactions, but may also alter the strength and direction of indirect effects (e.g., apparent competition, competitive displacement), both density- and trait-mediated, that are important for the structuring of parasitoid–host food webs (e.g., 83, 123, 183). Range expansions in response to climate change may result in escape from natural enemies (e.g., 116), as well as the accumulation of additional natural enemies (e.g., 10, 24, 115, 169), altering the magnitude and direction of direct competition (e.g., 29, 178), competitive displacement, or apparent competition. Insect communities experiencing the poleward range expansions that are expected under warming climate change scenarios will concurrently experience more extreme photoperiods, which are important for insect life-history and activity patterns. Nevertheless, empirical evidence of climate change effects on extrinsic competition among parasitoids and their consequences for host–parasitoid communities remain to be explored.

SUMMARY POINTS

1. Competition between adults can be broadly categorized as interference or exploitative. While examples of both forms abound for females, most studies of extrinsic competition between males have focused on interference competition, often lethal, for mates. Competition among females can be either inter- or intraspecific. Competition among males is almost exclusively intraspecific.

2. The type of competition exhibited by adult females depends strongly on correlated parasitoid life-history traits. Idiobionts (which tend to be ectoparasitoids) are far more likely to engage in interference competition such as brood guarding and fighting than are koinobionts (which are almost exclusively endoparasitoids). Both idiobionts and koinobionts engage in exploitative competition via a wide array of morphological and behavioral traits.

3. The morphological, physiological, and behavioral mechanisms underlying extrinsic competition between individuals translates into population- and community-level phenomena, including competitive displacement and apparent competition.

4. Competitive displacement and apparent competition are related phenomena in that species within a trophic level indirectly interact via another species in an adjacent trophic level. The species in the adjacent trophic level may determine the outcome of extrinsic competition between the first two species.

5. Anthropogenic stressors including habitat loss and fragmentation, invasive plants and animals, pesticides and fertilizers, and climate change gases are all expected to alter extrinsic competition and host–parasitoid food webs. Changes to volatile chemical complexity will alter the ability of parasitoids to efficiently forage for hosts and mates. Range expansions of hosts, parasitoids, and their natural enemies in response to changing temperatures will change the strength and direction of competitive interactions.

FUTURE ISSUES

1. How parasitoid foraging ability, in terms of the parasitoid's ability to distinguish signal from noise, is affected by the odor complexity resulting from multiple plant and herbivore species in the environment remains a question of fundamental importance in understanding how adult parasitoids engage in exploitative competition.

2. While examples exist, the ways in which morphological, physiological, and behavioral traits of competing species interact to result in community-level phenomena such as competitive displacement and apparent competition deserve further attention.

3. Increased focus on the prevalence of apparent competition and competitive displacement can improve our understanding of how host–parasitoid food webs are structured. Rigorous empirical field tests of apparent competition and competitive displacement theory will help.

4. Empirical tests of how extrinsic competition among parasitoids is altered by anthropogenic factors (habitat fragmentation, loss, or degradation; pesticides and fertilizer overuse; invasive species; and climate change) are needed.

5. We need to study how community-level phenomena of apparent competition and competitive displacement will respond to anthropogenic factors, especially species invasions and range expansions resulting from climate change. Such studies will be essential to understanding how host–parasitoid food webs will or will not be resilient to ongoing climate change and other anthropogenic factors.

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