

## Opinion

## Brood Parasites Are a Heterogeneous and Functionally Distinct Class of Natural Enemies

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Brood parasitism is the introduction of unrelated progeny into the nest or colony of a host that then raises the foreign young. This reproductive strategy has evolved independently and repeatedly among diverse animal taxa, and brood parasite–host interactions have become models for understanding coevolutionary arms races. Yet brood parasites have remained largely overlooked in previous syntheses of natural enemy ecology. Here, we argue that brood parasites are a heterogeneous and versatile class of natural enemies, blending traits characteristic of predators and trophic parasites. The functional distinctness of brood parasites reinforces the idea that natural enemies exist along a continuum rather than as a dichotomy. Brood parasite–host interactions can serve as valuable case studies to unify parasite–host and predator–prey theories.

## Brood Parasites Are Largely Overlooked in Natural Enemy Paradigms

**Natural enemies** (see [Glossary](#)) (i.e., **predators**, **trophic parasites** [hereafter, parasites] and **parasitoids**) are organisms that obtain resources from and negatively impact the fitness of their **victims** (i.e., **prey** and **hosts**). Seminal work by Lafferty and Kuris [1] characterized natural enemies by their **trophic strategy**, or the way in which they obtain foraging resources from their victims. Specifically, these authors proposed ten trophic strategies based on variation along four life-history axes: (i) the number of victims per life stage, (ii) the net effect on victim fitness, (iii) victim survival, and (iv) **intensity-dependent pathology**. These four axes can be used to distinguish the different types of natural enemies and their trophic strategies. A more recent review of natural enemy ecology [2] further highlighted three key ecological differences between parasites and predators: (v) relationship intimacy, (vi) relationship duration, and (vii) relative generation times. Two parallel conclusions emerged from these syntheses: although predators and parasites both negatively impact victim fitness, key factors reliably differentiate these classes of natural enemies.

How then do **brood parasites** – natural enemies that introduce their progeny into the hive or nest of an unrelated victim that then raises the brood parasite's young – compare to trophic parasites and predators? Despite their name, brood parasites are difficult to categorize as a class of natural enemies because they are a heterogeneous group. Some are **facultative** and some are **obligate brood parasites** [3–5]; some parasitize only conspecifics, others only heterospecifics, and some parasitize both [4,6,7]; some kill the adult victim and others do not [8,9]; some kill all of the host's young and some live alongside them [10,11]; some specialize on one species, and some attack diverse lineages [4,5,12]; and some live temporarily with their victims, while others do so permanently [13]. Perhaps because of their versatility and heterogeneity, brood parasites have been largely omitted from previous syntheses of natural enemy ecology, despite representing a widespread trophic strategy that has evolved independently and repeatedly in diverse animal lineages (Box 1, Table 1).

## Highlights

Adult brood parasites usurp the parental care of their hosts, which suffer fitness losses when raising brood parasitic progeny.

Brood parasites have been largely overlooked in previous theoretical and empirical syntheses of natural enemy ecology of trophic parasites versus predators.

We characterize brood parasites as a diverse and heterogeneous group of organisms that blend traits characteristic of both predators and trophic parasites.

Brood parasites are thus functionally distinct from predators and trophic parasites with respect to a broad array of their own life-history traits and impacts on hosts.

Brood parasites can serve to further unify natural enemy ecology and promote integration of parasite–host and predator–prey theories.

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### Box 1. Brood Parasites Are Diverse and Have Heterogeneous Impacts on Victim Fitness

Brood parasites are organisms that rely on **alloparental care** – that is, they introduce their young into the nests, hives, or broods of other organisms that then raise the foreign young. This parental strategy has evolved in a wide variety of arthropod taxa, including but not limited to social Hymenoptera [4,13,50], Hemiptera [51], Coleoptera [52], Lepidoptera [53], and Arachnida [54]. Ants alone are parasitized by an estimated 10 000 species of invertebrates [53], exemplifying the prevalence of social parasitism among insects. Alloparental care has also been documented in hundreds of fish species (reviewed in [55,56]) and evolved numerous times among birds [3,5].

Obligate brood parasites are organisms that depend exclusively upon interspecific alloparental care and exhibit no parental care of their own (Table 1). This strategy has evolved repeatedly in social insects (~88 independent origins; [75]), birds (~109 species from five different families; [5]), and at least one species of fish (the cuckoo catfish, *Synodontis multipunctatus*; [32,40]). Despite sharing a common reproductive strategy, obligate brood parasites are a diverse group of organisms with heterogeneous life histories and variable impacts on their victims' fitness. For example, obligate brood parasites vary widely in terms of host specialization [57] and the virulence of their impacts on host brood and on foster parents ([27]; Table 1).

### Brood Parasites Represent a Functionally Distinct Category of Natural Enemies

Brood parasites have been almost exclusively considered as functionally related to trophic parasites from a natural enemy perspective; accordingly, they have been used as study models of parasite–host systems towards understanding **coevolutionary arms races** [12,14–16]. Much of this body of literature has focused on the adaptations and counter-adaptations between obligate interspecific brood parasites and hosts, such as the parasites' visual or chemical host **mimicry** [8,17] and the antiparasitic **rejection** behaviors by hosts [12,18], as well as the evolution of **host resistance** and **host tolerance** [19,20].

Here, we argue that brood parasites represent a functionally distinct type of natural enemy, blurring the lines (*sensu* [21]) between parasites and predators. To support our case, we consider the seven life-history traits we highlighted from Lafferty and Kuris [1] and Raffel *et al.* [2] previously that are thought to differentiate parasites and predators. For each trait, we place brood parasites along the parasite–predator spectrum based on their behavior, ecology, and life-history.

#### Number of Victims per Life Stage

Many parasites typically attack only one victim per life stage, whereas predators feed on multiple victims [1]. In this regard, adult brood parasites more closely resemble predators than trophic parasites (Figure 1). For example, a single avian brood parasite can deposit its eggs in the nests of dozens of different hosts in a given breeding season and across its lifetime [22]. The same is generally true among fish and insect brood parasites, although **inquilines** – brood parasites that cohabitate with the host permanently inside its hive or colony – are a notable exception [23].

#### Net Effect on Victim's Fitness

Both parasites and predators have variable effects on victim fitness. A useful paradigm for understanding fitness impacts upon hosts and prey is the consumer–resource framework, recently proposed by Buck and Ripple [24], which explores the consumptive effects of natural enemies on their victims. Typically, parasites negatively impact host fitness by consuming somatic energy (i.e., direct ingestion of host body tissues) but the host stays alive. In contrast, parasitoids kill their hosts as a rule, and other parasites, such as **parasitic castrators**, reduce host fitness to nil by fully consuming the host's reproductive energy (i.e., diverting resources away from host reproduction) [25]. **Macropredators** also reduce victim fitness to nil by consuming their prey, whereas **micropredators**, such as mosquitoes, do not. In turn, brood parasites have a wide range of impacts on the victims' fitness, both across and within

### Glossary

**Alloparental care:** parental care of an offspring by a genetically unrelated parent.

**Brood parasite:** an organism that introduces its reproductive propagules into the brood of other organisms that then raise the foreign progeny.

**Coevolutionary arms race:** evolutionary feedback that involves counter-adaptations between interacting natural enemy–victim dyads, such as predator and prey, herbivore and plant, or parasite and host.

**Emery's rule:** the pattern among social insects whereby brood parasites share common ancestry and are often phylogenetically related to host species.

**Facultative brood parasite:** a brood parasitic species that sometimes deposits its eggs or young in the nests or colonies of other organisms but also exhibits parental care.

**Host:** a victim that harbors or nourishes a trophic or brood parasite.

**Host resistance:** a host response that either prevents or reduces the probability of parasitism occurring through counter-adaptations such as front-loaded (mobbing) defenses or parasitic egg recognition.

**Host tolerance:** a host response that prevents or reduces the negative fitness impacts of parasitism.

**Inquiline:** social insect brood parasites that live permanently in the victims' nests.

**Intensity-dependent pathology:** the impacts of the enemy on victim fitness increase with the intensity (e.g., number of enemies) of the attack.

**Landscape of disgust:** the theory that host species can perceive and respond to spatial variation in parasitism risk to reduce the probability of being parasitized.

**Landscape of fear:** the theory that prey species can perceive and respond to spatial variation in predation risk to reduce the probability of being depredated.

**Macropredator:** a predator that is comparable to or larger in body size than its prey.

**Micropredator:** a predator that is smaller in body size compared to its prey.

**Mimicry:** the evolved sensory matching of phenotypes between brood parasite young and host young to reduce the likelihood of rejection.

**Natural enemy:** an organism that obtains resources from, and negatively

species of brood parasites [26–28]. For example, brood parasitic adult birds do not generally kill adult hosts (although there may be possible exceptions; [29]), but rather partially divert reproductive energy intended for host young, representing a hybrid between trophic parasites (which consume somatic energy) and parasitic castrators (which consume all of the host's reproductive energy). Critically, the tendency to reduce host fecundity vs. host survival can have important implications for population dynamics between natural enemies and their victims. For example, trophic parasites that impact host fecundity tend to generate more cyclical dynamics than those that impact host survival [30], and the exploration of these dynamics is also warranted in brood parasites. However, some obligate brood parasitic young, including the infamous hatchlings of the common cuckoo (*Cuculus canorus*), evict or otherwise kill all of the host parents' nestlings [3], reducing foster parental reproductive success of the parasitized brood to nil, as do macropredators, parasitoids, and parasitic castrators. In contrast, other brood parasitic young remove only part of the host's brood or clutch or do not directly kill the host progeny at all but coexist and compete for resources with them [23,25,31]. Impacts on victim fitness can vary even within a single brood parasite species – for example, the young of the obligate brood parasitic cuckoo catfish (*Synodontis multipunctatus*) can consume some or all of its mouthbrooding cichlid host's eggs [32].

### Victim Survival

Hosts generally survive interactions with parasites but do not do so with parasitoids or predators. In turn, brood parasites run the gamut with respect to their impacts on victim survival. For instance, several adult avian and social insect brood parasites manipulate or eliminate host clutch/eggs and brood sizes through farming or mafia tactics (Box 2). However, most avian foster parents (host adults) raising brood parasitic young are not killed directly by the foreign progeny but still may themselves suffer fitness-relevant physiological costs due to fostering brood parasitic young. For example, adult male prothonotary warblers (*Protonotaria citrea*), when experimentally parasitized by nest-sharing brown-headed cowbirds (*Molothrus ater*), exhibit higher baseline corticosterone levels, reduced body mass, dampened immune function, and lower interannual return rates, compared to nonparasitized parental males [33,34]. This pathology is similar to that of trophic parasites, which are also associated with widespread increases in glucocorticoids among vertebrate hosts [35]. In contrast, even some particularly virulent brood parasites can impose little to no physiological cost on host adults. Accordingly, parasitism of Reed Warblers (*Acrocephalus scirpaceus*) by nestmate-evictor common cuckoos did not have any discernible negative effects on adult body mass or physiological condition [36]. In turn, some brood parasitic Hymenoptera typically kill the resident (host) queen and take over her egg-laying duties, leaving the host workers to raise the parasitic progeny [4,37]. However, host and parasite queens can coexist temporarily in some paper wasps [4] and/or long-term in ants [23]. Among the latter, some species of parasitic workers elicit regurgitations, imposing foraging and energetic costs upon host workers.

### Intensity-dependent Pathology

Among the trophic strategies characterized by Lafferty and Kuris [1], solitary predators, parasitoids, some micropredators, and parasitic castrators exhibit intensity-independent pathology (whereby the impact/**virulence** does not increase in proportion to the number of enemies attacking the same prey/host). In contrast, most other parasites, social predators, and some micropredators exhibit intensity-dependent pathology (whereby the impacts of the enemy on victim fitness increase with the number of attackers or the intensity of the attack). Similar to trophic parasites, brood parasites largely exhibit intensity-dependent pathology – the more brood parasitic propagules, per nest, the lower the fitness of the host (e.g., [31,38,39]). For example, some species of dulotic ants can invade multiple independent nests of a single

impacts the fitness of, its victims (i.e., predator, parasite, or parasitoid).

**Obligate brood parasite:** a brood parasite that exclusively deposits its young in the nests of other (interspecific) organisms and never exhibits parental care.

**Parasitic castrator:** a trophic parasite that blocks the reproduction of its host.

**Parasitoid:** a trophic parasite with high virulence that eventually kills its host.

**Predator:** a natural enemy that partially or completely consumes its victim.

**Prey:** a victim that nourishes a predator.

**Rejection:** the ability of a host parent to recognize and eliminate the foreign brood parasite progeny (egg or young).

**Social parasite:** an organism that lays its eggs in the hive, colony, nest, brood, or clutch of others; usually used as equivalent of 'brood parasite' for social insect species.

**Trophic parasite:** a parasite that lives on or in the host and consumes host resources.

**Trophic strategy:** the way in which a natural enemy obtains foraging resources from its victim.

**Victim:** an organism whose fitness is negatively impacted by a natural enemy (i.e., prey, host).

**Virulence:** the magnitude of a parasite's negative impacts on host fitness.

Table 1. A Representative List of Obligate Interspecific Brood Parasites and Their Hosts

Brood parasite	Number of brood parasite species	Number of host species	Specialization	Primary victims	Impact on host adult	Impact on host brood	Specialized adaptations	Refs
Paper wasps (genus <i>Polistes</i> , subfamily Polistinae)	3	5	Variable	Other <i>Polistes</i>	Kills host queen, workers tend parasitic brood; few cases of cohabitating with host queen	Kills some to all of the host brood	Chemical mimicry; morphological adaptations to facilitate usurpation	[4]
Yellowjackets, hornets (subfamily Vespinae)	5	<20	Variable	Closely related Vespinae	Kills host queen, workers tend parasitic brood	Kills some to all of the host brood	Chemical mimicry; morphological adaptations to facilitate usurpation	[37,72,73]
Allodapine bees (subfamily Xylocopinae)	17	17	Variable	Closely related Xylocopinae	Decrease fitness of adult host	Vague, but seems that brood are cohabitating without causing mortality in host	Strongly reduced scopa and mouthparts (i.e., incapable of rearing own brood); enlarged legs and modified mandibles to facilitate excavating burrows in wood	[74,75]
Cuckoo bumblebees (genus <i>Bombus</i> )	31	>50	Variable	Other <i>Bombus</i>	Usually kills host queen, workers tend parasitic brood	Large range, sometimes kills and/or eats all brood, other times leaves some host brood and or/queen alive in a few cases	Chemical mimicry, insignificance and/or camouflage; morphological adaptations to facilitate usurpation; enlarged Dufour gland produces a repellent chemical for protection against host worker attacks.	[50,75]
Ant temporary <b>social parasites</b>	~200	>200	Mostly specialist	Other ants	Often kills the host queen, and functionally replaces it; host workers raise parasitic brood	Host workers are gradually replaced by parasitic workers	Chemical insignificance; parasitic species of <i>Lasius</i> and <i>Bothriomyrmex</i> kill the host queen by decapitation or throttling	[13,23,75]
Ant dulotic social parasites	80	>80	Mostly specialist	Other ants	Kills host workers that are defending raided colonies	Some host brood is eaten, but the majority is transported to eclose inside host nest and act as workers	Chemical mimicry; mass raids into host nests; saber-shaped mandibles in workers of <i>Strongylognathus</i> and <i>Polyergus</i> , which preclude them from feeding themselves, making them dependent on host workers	[13,23,75]
Ant inquiline social parasites	100	>100	Mostly specialist	Other ants	Most species coexist with the host queen and adult workers	Host queen is allowed to produce workers constantly	Have lost worker caste partially or completely, making them dependent on their hosts permanently; reduced mouthparts and body size, smooth cuticles	[13,23,75]
Cuckoo catfish ( <i>Synodontis multipunctatus</i> )	1	<5	Specialist	Mouthbrooding cichlids (Cichlidae)	None documented	Variable; kills some to all of the host brood	Disrupts host spawning and rapidly lays eggs among host eggs	[32,40,76]
Black-headed duck ( <i>Heteronetta atricapilla</i> )	1	<20	Generalist	Ducks/swans (Anatidae), rails (Rallidae), and gulls (Laridae)	None documented	Leaves host brood soon after hatching; minimal costs besides loss of incubation efficiency	None documented; this is the only precocial avian obligate brood parasite	[5,6]

Table 1. (continued)

Brood parasite	Number of brood parasite species	Number of host species	Specialization	Primary victims	Impact on host adult	Impact on host brood	Specialized adaptations	Refs
Cuckoos (family Cuculidae)	65	>100	Variable	Passerine birds (order Passeriformes)	Increased stress-induced corticosterone	Variable; some kill and others coexist with host brood	Egg visual mimicry; nestling acoustic mimicry; egg eviction via egg dumping	[5,77]
Honeyguides (family Indicatoridae)	17	<30	Variable	Nonpasserine birds	None documented	Kills all of the host brood	Egg visual mimicry, hooked bill used to puncture eggs and/or kill nestlings	[5]
Indigobirds (family Viduidae)	20	<50	Mostly specialist	Estrildidae	None documented	Mostly coexists with host brood	Nestling gape and acoustic mimicry	[5]
Cowbirds (family Icteridae)	6	>200	Mostly generalist	Passerine birds (order Passeriformes)	Decreased body condition and immune function; increased baseline corticosterone; reduced interannual return rates	Outcompetes some to all of the host brood	Fledgling visual mimicry in the specialist species	[5,31,33,34]

host species, or instead parasitize multiple host species to maintain enough host workers to rear their brood [23].

#### Relationship Intimacy

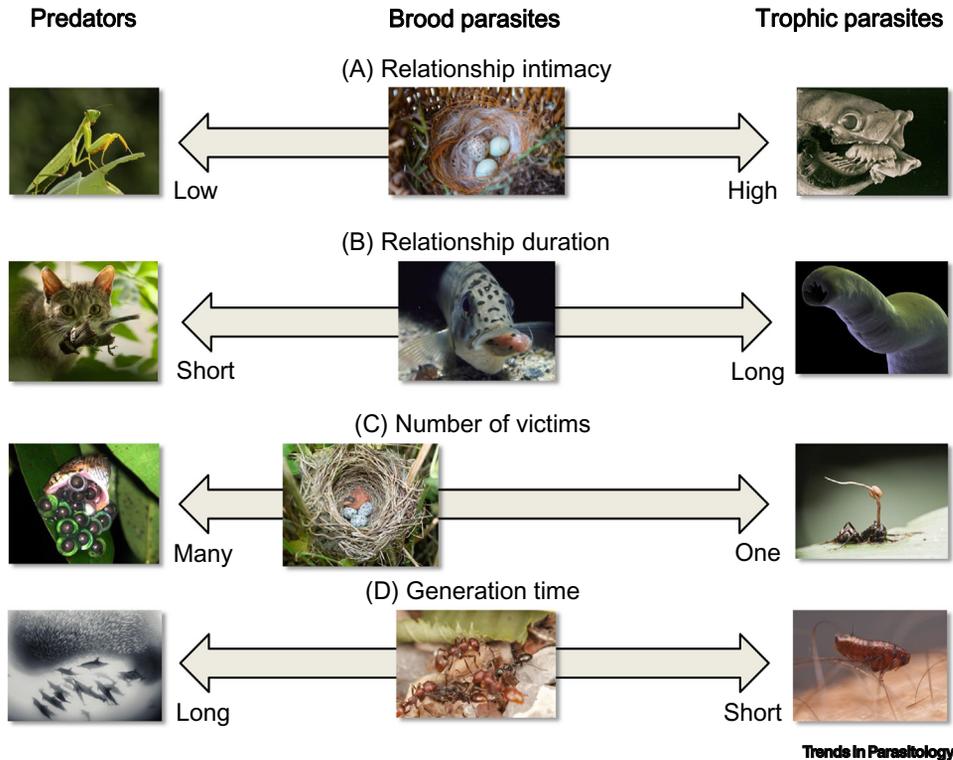
Raffel *et al.* [2] argued that, unlike predators, parasites have a fundamentally more intimate relationship with their victims than predators because they live on or inside of the host. Brood parasites generally live with the victim rather than on or in the victim (Figure 1), representing an intermediate level of intimacy. A notable exception is the fry of the brood parasitic cuckoo catfish, which cohabit with, and prey upon, the young of their mouthbrooding cichlid host inside the host's buccal cavity [32,40]. Nevertheless, it could be argued that brood parasites are more intimate with their hosts than they ostensibly appear to be because they inhabit the nest or the hive, each of which is a critical aspect of extended phenotype of birds or social insects (e.g., [41]).

#### Relationship Duration

Predators generally have short, transient relationships with prey, whereas parasites tend to have longer and more durable relationships with hosts [2]. In turn, brood parasites interact with their victims during their own early stages of life (birds: egg, nestling, and fledgling stages; fish: egg and fry stages; insects: egg and larval stages) but many live independently from their hosts as adults, representing an intermediate relationship duration between predators and parasites (Figure 1). However, their longer affiliations with victims across ontogenetic stages, especially when cohabitating with host progeny (eggs and/or care-dependent juveniles), can facilitate brood parasitic adaptations such as egg, nestling, and/or fledgling mimicry [42] and, in turn, coevolutionary arms races.

#### Generation Time

Parasites are usually smaller and have faster generation times than their hosts, whereas predators are typically larger with slower generation times [2]. As a result, parasites often have an inherent advantage in coevolutionary arms races [43]. In contrast, brood parasites are often of similar body size and generation time to their victims, resulting in similar speeds of intergenerational adaptation [44] in coevolutionary arms races (Figure 1).



**Figure 1. Selected Axes of Trait Variation among Natural Enemies.** (A) Relationship intimacy. Trophic parasites tend to have more intimate relationships with their victims than predators [2]. For example, parasites such as the tongue-eating louse (*Cymothoa exigua*) consume and then functionally replace their hosts' tongues, whereas predators such as praying mantises have only a brief, external interaction with their prey. Brood parasites such as brown-headed cowbirds (*Molothrus ater*) lay their eggs in the nests of their hosts, representing an intermediate level of relationship intimacy. (B) Relationship duration. Parasites tend to have longer lasting and more sustainable relationships with their victims than predators [2]. For example, hookworms can live within their human hosts for years, whereas predator-prey interactions are generally transient and often result in the death of the victim, such as with domestic cats and songbirds. In turn, brood parasites, including *Synodontis* catfish fry (that consume unhatched host eggs while inside their mouthbrooding cichlid host), spend their early life stages with victims but do not live in or with them permanently, representing an intermediate relationship duration. (C) Number of victims. Within a given life stage, parasites tend to have one victim, whereas predators can attack multiple victims [2]. For example, the entomopathogenic fungal parasite *Ophiocordyceps* infects only one individual ant, whereas a snake can consume dozens of frog eggs in one sitting. Brood parasites more closely resemble predators in this regard, with individuals like the common cuckoo (*Cuculus canorus*) depositing their eggs in the nests of multiple hosts throughout their lifetimes. (D) Generation time. Parasites tend to have shorter generation times than their hosts, which provide them with an advantage in coevolutionary arms races [2]. For instance, an adult female human flea (*Pulex irritans*) can lay 50 eggs a day on a daily basis for 40 days, producing 2000 eggs in its lifetime, compared to a global fertility of an average of 2.4 children/lifetime of their human hosts. In contrast, predators tend to have longer generation times than their hosts. For example, common dolphins (*Delphinus delphis*) give birth to only one offspring every 1–6 years, whereas the fish they eat reproduce multiple times per year and produce thousands of eggs at a time. Brood parasites such as dulotic ants (*Polyergus rufescens*) are often closely related evolutionarily and therefore have similar generation times to their victims (**Emery's rule**), somewhat limiting advantages against their victims in coevolutionary arms races relative to trophic parasites.

### Concluding Remarks

Using the paradigms proposed in Lafferty and Kuris [1] and Raffel *et al.* [2], we have demonstrated that brood parasites defy categorization as natural enemies with respect to canonical differences between trophic parasites and predators. The blurred lines between parasitism and predation evident among brood parasites reinforce the idea of a natural enemy continuum [1].

### Outstanding Questions

Do coevolutionary arms races between brood parasites and hosts more closely resemble those between predators and prey or trophic parasites and hosts?

Do patterns of coevolution between brood parasites and hosts cycle as they do in some predator-prey systems?

Do mafia or farming strategies by brood parasites result in coevolutionary arms races?

Under what ecological scenarios do host specialization and sensory mimicry evolve (or not) in brood parasites?

Are anecdotal reports of brood parasitism in parental frogs representative of evolved parasitism or opportunism?

What are the genomic and developmental bases of facultative vs. obligate brood parasitism in insects and birds relative to sister lineages with parental care?

Are the sensory requirements of detection and recognition similar between hosts and parasites to those in predator-prey and trophic parasite-host systems?

How do brood parasitic offspring overcome species recognition issues associated with being raised by another species?

Are adult generalist obligate brood parasites more likely to parasitize the host species that raised them than other potential hosts?

Do brood parasites generate cyclical population dynamics with their host species, as do trophic parasites that impact host fecundity rather than host survival?

How do brood parasites fit into the consumer-resource framework?

How do host species integrate the 'landscape of fear' and 'landscape of disgust' to respond to spatial variation in brood parasitism risk?

### Box 2. Farming, Mafia, and Other Tactics of Adult Brood Parasites That Reduce Host Fitness

Host fitness losses are overwhelmingly caused by brood parasite young, which reduce or eliminate the reproductive success of the parasitized nests or hives. However, adult brood parasites, usually females, can also induce host fitness losses through several ancillary strategies and tactics.

#### Egg Destruction

To reduce competition with the host and, in the case of multiple parasitism, with competing parasitic progeny [58], adult avian brood parasites may peck and render host eggs unviable in the nest where and when they lay their own parasitic egg [59]. Similarly, social insect parasites destroy host eggs and young larvae [4,50], in some cases, sparing older host brood that will shortly become adult workers that will rear parasitic brood [60].

#### Egg Consumption

Brood parasites may consume host eggs; this behavior is known to be most common in social insect parasites [4,10,50] whereas it has only rarely been documented among avian brood parasites [61].

#### Egg Replacement

To reduce visual or tactile cues of parasitism having taken place [62], adult avian brood parasites may remove a host egg when laying their own [63].

#### Farming Behavior

When avian brood parasites encounter host nests too late for successful parasitism (i.e., too far into the incubation period; [64]), they may generate future opportunities for parasitism by destroying the ongoing breeding attempt and forcing hosts to re-nest [65,66].

#### Mafia Behavior

To retaliate against rejecter hosts that eliminate parasitic progeny from the nest [67], adult brood parasites of several bird species are reported to destroy and terminate the ongoing breeding attempt, forcing the host both to re-nest and to shift their rejection behavior to acceptance [65,68]. Similarly, if social insect parasites cannot completely suppress ovarian development in workers [69] they may control host reproduction by eliminating host brood, which has been documented in brood parasitic ants, bumblebees, and paper wasps [4,70,71].

Because of the taxonomic diversity of brood parasites and their highly variable impacts on victim fitness, we consider that they present a unique opportunity to further unify predator–prey and parasite–host theories. The similarities between parasites and predators have long been recognized (reviewed in [2]), and we argue that comparative studies among different types of brood parasites or between brood parasites and other natural enemies can shed light on new avenues in this area of research (see Outstanding Questions). For example, a recent paper proposed the concept of **landscape of disgust** – the idea that host species can perceive and respond to spatial variation in parasitism risk to reduce the probability of being parasitized [45]. This concept is directly analogous to and derived from the **landscape of fear**, which posits the same for prey responding to predators [46]. Both ideas have been previously treated in the brood parasite literature [47,48], although they have not been linked to the broader theory and body of literature related to either concept. Brood parasites can thus serve as valuable case studies to unite these two frameworks into a combined ‘landscape of peril’ (*sensu* [49]) and explore similarities or differences in avoidance behavior of victims to distinct types of natural enemies. Similarly, explicit inclusion of brood parasites into the consumer–resource framework proposed by Buck and Ripple [24] would be a fruitful avenue towards a deeper and more synthetic understanding of natural enemy ecology by exploring the similarities and differences between traditional somatic trophic parasitism and reproductive trophic parasitism of brood parasites.

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### Declaration of Interests

There are no interests to declare.

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