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.

1Department of Ecology, Evolution and Behavior, School of Integrative Biology, University of Illinois at Urbana-Champaign, 515 Morrill Hall, 505 S. Goodwin Ave., Urbana, IL 61801, USA
2Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, 615 E. Peabody Dr., MC-650, Champaign, IL 61820, USA
3Department of Biology, University of Rochester, 402 Hutchison Hall, P.O. Box 270211, Rochester, NY 14627, USA

*Correspondence: henry.s.pollock@gmail.com (H.S. Pollock).
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 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 [55], 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; [6]), and at least one species of fish (the cuckoo catfish, Synodontis multipunctatus; [52, 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 [22; Table 1].

**Brood Parasites Are Diverse and Have Heterogeneous Impacts on Victim Fitness**

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 attractants [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.

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**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 *inquiline* brood parasites that cohabitate with the host permanently inside its hive or colony – are a notable exception [23].

**Net Effect on Victim’s Fitness**

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

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

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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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