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Review Article

The ants (Hymenoptera: Formicidae) and their parasites: effects of parasitic manipulations and host responses on ant behavioral ecology

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Abstract

Ants can display modified behaviors that represent the extended phenotypes of genes expressed by parasites that infect them. In such cases, the modifications benefit the parasite. Alternatively, displayed behaviors can represent host responses to infection that benefit colony fitness. Though some enigmatic examples of behavioral manipulation have been reported, parasitism of ants and its effects on ant behavior and ecology are generally poorly understood. Here, we summarize some of the present-day literature on parasite-ant interactions. Our main focus is on interactions that change host behavior so drastically that infected ants play a seemingly different societal and, perhaps, ecological role. We highlight the parallels that can be found across parasite-ant symbioses that result in manipulated behaviors, such as summiting, phototaxis, substrate biting, and wandering. We also point out the many present knowledge gaps that could be filled by efforts ranging from novel parasite discovery, to more detailed behavioral observations and next-generation sequencing to start uncovering mechanisms.

Key words: Parasites, ants, behavior, extended phenotype, manipulation, review.

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Introduction

Parasites exploit all free-living organisms and comprise the majority of species on Earth (Windsor 1998, Schmid-Hempel 2011). Their biomass in ecosystems is substantial, and they play important ecological roles in shaping communities (Kuris & al. 2008). One of the best investigated social insects, *Apis mellifera* Linnaeus, 1758, has over 70 described macro- and micro-parasites (Schmid-Hempel 1998). While this number is impressive, it is likely an underestimate and not unique to *A. mellifera*. Other social insect hosts, with societies equal in complexity and size, have few or no reported parasite species. This may be attributed to a lack of commercial interest and limited funding for such investigations, instead of a true lack of parasites (Schmid-Hempel 2011). The high levels of biodiversity and biomass of parasites alter energy flux to other trophic levels and change community structure through modified competitive abilities. Behavior is central to enormous impacts on host growth rates as it influences factors such as seed dispersal, prey capture, and soil excavation. Beyond the consumptive effects of parasites, host energy can be drained further by reallocating energy to the display of resistance behaviors (Rigby & al. 2002). Furthermore, parasites that modify the behavior of intermediate hosts, to ascertain trophic transmission to ultimate host predators, drastically affect food webs (Lafferty & Morris 1996). In fact, parasites can alter the behavior of their host to such an extent that they change its ecological function as infected animals can react differently to abiotic stimuli compared to their conspecifics. They can also display different activity levels, sounds, smells, distribution, and social roles (Moore 1995).

While parasites are biomass rich, so are ants (Fittkau & Klinge 1973, Erwin 1989). Ants are among the most abundant animal groups and often comprise more than 80% of the arthropods in tropical rain forests (Hölldobler & Wilson 1990, Davidson & Patrell-Kim 1996). This success can be attributed to their complex social organization and intriguing behavioral ecology. Ant species display an array of unique behaviors that should be studied at the individual, caste, and colony level, then

placed in the context of the species' natural environment (Sudd & Franks 1987). Parasites are key components of that environment as they influence ant behaviors by providing pressures that select for adaptive host behavioral traits, such as parasite recognition, prevention, and defense (Lozano 1991, Agnew & al. 2000). In addition to displaying behaviors that protect individuals and the colony against parasites, infected ants can also be viewed as the parasites' extended phenotype and display behaviors that benefit the parasite's life cycle and transmission (Dawkins 1982). Such manipulated behaviors can be very apparent, such as the novel, fungus-induced substrate biting behavior observed in infected worker ants that are thought to be mainly of the foraging caste (Boer 2008, Andersen & al. 2009). Modifications can also be subtler, as described for a cestode that reduces activity of infected individuals of the nursing caste and aggression displayed by uninfected nestmates, to seemingly facilitate trophic transmission towards the woodpecker host (Plateaux 1972, Scharf & al. 2012, Beros & al. 2015). The altered behavior of infected individuals, such as reduced or less effective foraging activity, could thus impact the fitness of the colony as a whole. Parasites could also affect behavior at the colony level, for instance, through changes in the chemical profiles of infected individuals, as reported for certain ectoparasites (e.g., Csata & al. 2017). This makes the colony's gestalt odor (i.e., the uniform odor of a colony) more heterogeneous and relaxes the margin of error used by uninfected nestmates when assessing chemical profiles to distinguish kin from non-kin. This could lead to increased susceptibility to competing conspecifics, social parasites and parasitoids that drain the colony's resources and reduce colony fitness. Alternatively, certain behavioral responses to infection might represent mere side-effects without clear functions. Deciphering where parasitic manipulation begins and host response ends is, thus, a complicated endeavor that requires thorough experimentation to determine which of the interacting organisms, if at all, adaptively benefits from the altered behavior.

Behavioral changes are especially important to consider in ants because of their role as ecosystem engineers (Folgarait 1998, Griffiths & al. 2018). Ants are responsible for a substantial part of the nutrient redistribution performed by animals in the rainforest. Moreover, their removal of food resources is not compensated by other invertebrates and vertebrates when ants are removed from a habitat. This makes them key players in maintaining rainforest ecosystem processes (Griffiths & al. 2018). Modifications of ant behavior, to either avoid or as a result of infection, might impact such ecosystem processes. However, research linking parasite pressures and infection levels to resulting ant behaviors and their possible ripple effects throughout ecosystems have not been conducted yet. To better understand these effects and their evolutionary basis, rigorous investigations of parasites and their level of influence on host behavior are thus warranted (Weinersmith & Earley 2016).

In recent years, manipulating parasites and their hosts has gained the interest of researchers and the general public. New manipulative species interactions are being discovered (Steinkraus & al. 2017). Yet, there are many significant outstanding questions, even in systems that were described decades ago (Badie & al. 1973, Loos-Frank & Zimmermann 1976, Romig & al. 1980). Next-generation sequencing has made it possible to unveil gene expression and potential mechanisms underlying parasitically altered host behaviors (de Bekker & al. 2015, Malagocka & al. 2015, Feldmeyer & al. 2016). Such efforts can reveal how and when parasites influence host activity, especially in organisms that are as experimentally approachable as ants. We aim to create a broader interest in parasite-ant interactions by summarizing what is known and highlighting knowledge gaps waiting to be filled. We hope to entice more myrmecologists and behaviorists to integrate the effect that parasites might have on the behavior and biology of their focal ant species.

Parasites influencing ant behavior

Phenotypic changes in the host – as a result of parasite pressures and infection – can be adaptive to that host and aid its survival. Alternatively, parasites can manipulate host physiology, morphology, life history, and behavior, to directly benefit their own survival (Poulin & Thomas 1999, Thomas & al. 2010). Adaptive manipulation of host behavior can range from slight changes in existing behaviors to the induction of completely novel ones (Poulin 1994, Thomas & al. 2002). Ants are favorable parasite targets because of their dominance in most ecosystems and ubiquity among habitat types. Furthermore, because of their social tendencies (e.g., nest living, food sharing, brood care), ant societies can spread parasites among colony members (Cremer & al. 2007, Hughes 2012, Konrad & al. 2012, Beros & al. 2015). As such, parasite-induced behavioral shifts in ants have been widely reported. However, we suspect the records to be far from complete (Schmid-Hempel 1998). We summarize and discuss some of the present-day literature on entomopathogenic viruses, prokaryotes, fungi, protozoans, helminths, and insects, with our main focus on those that manipulate ant behavior. This reveals that information on ant-infecting viruses, prokaryotes, and protozoans is largely lacking. More in-depth research on fungi, helminths and parasitizing insects is actively underway. Moreover, this review demonstrates the parallels between observed manipulated behaviors caused by parasites across taxa (Tab. 1). Such parallels include climbing and biting vegetation by infected individuals, reduced aggression levels and task abandonment, and wandering behavior.

Viruses: Massive declines in honeybee populations have prompted the characterization of insect parasites and their effects on individual and colony-level fitness. Additionally, the search for effective biocontrol agents against insect pests provides a primary motivation to study entomopathogenic viruses. This motivation has led to in-depth studies on baculoviruses (double stranded

Tab. 1: Summary of ant hosts and their manipulative parasites detailed in this review.

Host subfamily	Host genus	Parasite		Reported manipulation
Dolichoderinae	*Dolichoderus*	*Ophiocordyceps*	(Fungus)	elevation seeking, biting
Formicinae	*Camponotus*	*Brachyleicthum mosquensis*	(Helminth)	elevation seeking
		Dicrocoelium hospes	(Helminth)	elevation seeking
		Ophiocordyceps	(Fungus)	task abandonment, increased (early infection) and decreased (late infection) nest occupation, elevation seeking, light seeking, hyperactivity, biting
	Colobopsis	*Mermis*	(Helminth)	water seeking
		Ophiocordyceps	(Fungus)	elevation seeking, biting
	Formica	*Dicrocoelium dendriticum*	(Helminth)	elevation seeking, biting
		Elasmosoma michaeli	(Insect)	aggregation
		Pandora	(Fungus)	elevation seeking, biting
	Lasius	*Pheromermis villosa*	(Helminth)	water seeking
	Oecophylla	*Ophiocordyceps*	(Fungus)	elevation seeking, biting
	Polyrhachis	*Ophiocordyceps*	(Fungus)	elevation seeking, biting
Myrmicinae	*Cephalotes*	*Myrmeconema neotropicum*	(Helminth)	gaster flagging, reduced alarm response, reduced aggression
		Ophiocordyceps	(Fungus)	elevation seeking, biting
	Daceton	*Ophiocordyceps*	(Fungus)	elevation seeking, biting
	Solenopsis	*Pseudacteon tricuspis*	(Insect)	increased nest occupation, reduced aggression, microclimate seeking, timed dispersal from nest
		Strepisiptera: Myrmecolacidae	(Insect)	elevation seeking, light seeking
	Temnothorax	*Anomotaenia brevis*	(Helminth)	increased nest occupation, task abandonment, reduced alarm response, colony reduced aggression
	Trachymyrmex	*Megalomyrmex adamsae*	(Insect)	colony reduced reproduction (gyne castration)
Paraponerinae	*Paraponera*	*Ophiocordyceps*	(Fungus)	elevation seeking , biting
Ponerinae	*Pachycondyla*	*Myrmecolax incautus*	(Insect)	increased nest occupation, task abandonment, elevation seeking, hyperactivity

DNA viruses) that are effective enough to cause epizootics (i.e., insect epidemics) (Vega & Kaya 2012), as seen in infected caterpillars with "tree-top disease" (Goulson 1997, Hoover & al. 2011). Baculovirus-infected lepidopteran larvae display hyperactive behavior that results in higher dispersal rates compared with uninfected larvae. Additionally, unlike healthy larvae, infected individuals summit to the top and edge of plant leaves. These behaviors are thought to optimize dispersal of viral disease particles over a larger area and onto the plant foliage below (Goulson 1997, Kamita & al. 2005, Hoover & al. 2011, van Houte & al. 2012). The baculovirus gene *ecdysteriod uridine 5'-diphosphate-glycosyltransferase* (*egt*), appears to be essential for the observed climbing behavior seen in caterpillars (Hoover & al. 2011). The gene encodes for the enzyme EGT, which is known to inactivate the molting hormone 20-hydroxyecdysone (20E) in the host (Riddiford & al. 2003). Indeed, RNAi-mediated knockdown and hormone-treatment assays showed that the regulation of 20E is involved in virus-induced tree-top disease (Zhang & al. 2018). Nevertheless, this extended phenotype of viral *egt* appears to be species specific. Its effects are not observed for all baculovirus-caterpillar interactions (Ros & al. 2015). Expression of the viral gene *protein tyrosine*

phosphatase (ptp) appears to be a more conserved host manipulation strategy among baculoviruses that infect lepidopterans (van Houte & al. 2012). It induces enhanced locomotory activity in infected larvae and causes them to display wandering behavior (Kamita & al. 2005). Such hyperactivity is also observed in ants that are affected by certain fungal parasites and parasitoids (see Tab. 1 and sections Fungi as well as Insect parasites below). Moreover, light has been suggested to play a key role in wandering activity and the synchronized timing of baculovirus-induced ascension. Hyperactivity intensified under light conditions, and infected larvae showed positive phototropism (van Houte & al. 2014, Han & al. 2017). Similar influences of light on fungus-infected and trematode-infected ants have also been reported (see Tab. 1 and sections Fungi as well as and Helminths below). Moreover, the activation of *ptp* homologs in *Ophiocordyceps*-manipulated carpenter ants (see section Fungi) have also been found (de Bekker & al. 2015). This suggests that similar mechanisms could be underlying behavioral modifications that show parallels across different parasite-host interactions.

Conspicuous extended phenotypes, induced by viruses, have not yet been reported for ants. However, this could be due to the fact that only a handful of the ant-associated viruses that likely exist have been found. Early studies have described "virus-like particles" in ants (Steiger & al. 1969, Avery & al. 1977). This was later followed by studies on viral infections in ants with a specific baculovirus to identify possible biocontrol agents (Dhandapani & al. 1994, Li & al. 1999), which has also sparked the discovery of the Solenopsis invicta viruses (SINVs) that infect the imported fire ant *Solenopsis invicta* Buren, 1972 (see Valles & al. 2004, Valles & Strong 2005, Valles & al. 2007, Valles & Hashimoto 2009). More recent studies have revealed additional ant viruses (Valles & al. 2013, Valles & al. 2016, Olendraite & al. 2017, Valles & al. 2018) as well as novel strains of viruses (Sébastien & al. 2015) that have been linked to the massive worldwide decline of honeybees (de Miranda & Genersch 2010). These recent identifications demonstrate the likely ubiquity of viral pathogens in ants waiting to be discovered. Among the known ant viruses, the single-stranded RNA viruses that infect the imported fire ant *S. invicta* (SINV-1 and SINV-1A; SINV-2; SINV-3) (Valles & al. 2004, Valles & Strong 2005, Valles & al. 2007, Valles & Hashimoto 2009) are probably best described. All three viruses (SINV-1, -2, and -3) are present in field colonies of *S. invicta* (see Porter & al. 2013) and are found in all developmental stages (Valles 2012). Viral effects on ant behavior at the individual and colony level are generally not well understood. However, in *S. invicta*, there is some evidence for colony-level behavioral effects of infection. One study revealed that SINV-1 weakened the competitive ability of *S. invicta*, despite infection symptoms being hardly discernable. This made the colony more susceptible to elimination by sympatric ant species (Chen & al. 2011). Investigating how this behavioral effect could benefit the SINV-1 virus, if at all, could be an interesting follow-up study. The pathogenicity of SINV-3 is more apparent. Infection in the colony results in large numbers of dead ants and brood, followed by colony collapse (Porter & al. 2013). The queens of SINV-3-infected colonies undergo weight loss and produce fewer eggs (Valles & al. 2014). These disease outcomes appear to be related to changes in feeding behavior in infected workers, which leads to deprivation of protein in larvae and the queen (Valles & al. 2014). If any of these behaviors have an adaptive benefit to the virus or if they are mere symptoms of infection is also unknown. Further studies that would start to distinguish these scenarios by addressing optimal conditions for virus particle transmission would enrich our knowledge of viral infections in *S. invicta* communities.

While non-model systems can yield critical information about key biological questions (Russell & al. 2017b), insect species with little commercial interest are less valued and are often seen as unimportant (Dunn 2005). Thus, current knowledge on viruses affecting ants has been driven largely by the urgency for the biological control of invasive species. A diversity of ants, however, are key players in ecosystem maintenance and functioning (Folgarait 1998, Griffiths & al. 2018). Identifying viruses and understanding how viral infections affect ant behavior at the individual and colony level are warranted. Studying many systems – not just those of economic value – will provide a broader foundation for more applied and urgent needs. Metagenomic and bioinformatic approaches have revolutionized the rate of viral discovery and are currently widely applied to characterize the viral ecology of infectious diseases (Dutilh & al. 2017). Moreover, these characterizations might lead to the unveiling of pathogens related to the baculoviruses that infect lepidopterans or completely novel ones that induce parallel behavioral manipulations. Such discoveries could be followed by comparative studies that make use of next-generation sequencing to reveal mechanisms underlying such extended phenotypes and their possible convergent evolution.

Prokaryotes: The characterization and transmission of ant-associated bacteria have been studied in a variety of ant systems (Ishak & al. 2011, Andersen & al. 2012a, Kautz & al. 2013, Liberti & al. 2015, Zhukova & al. 2017). Although descriptive studies based on pyrosequencing of 16S rRNA gene amplicons provide an important overview of the microbiota, they do not address the biological relevance of the bacteria discovered (i.e., metabolic capabilities and function) (Engel & al. 2012). Bacteria such as *Spiroplasma* Saglio, 1973 and *Wolbachia* Hetrig & Burt, 1924 associate with a wide variety of insects (Hilgenboecker & al. 2008, Zug & Hammerstein 2015) and are found in the gut or haemolymph (Engel & Moran 2013). While *Wolbachia* strains infect a diversity of ant species (Wenseleers & al. 1998, Frost & al. 2010, Ramalho & al. 2017a, b), their prevalence can vary among castes within colonies, among colonies within populations, and among species (Wenseleers & al. 1998, Russell & al. 2009, Russell 2012). In some species, *Wolbachia* are even

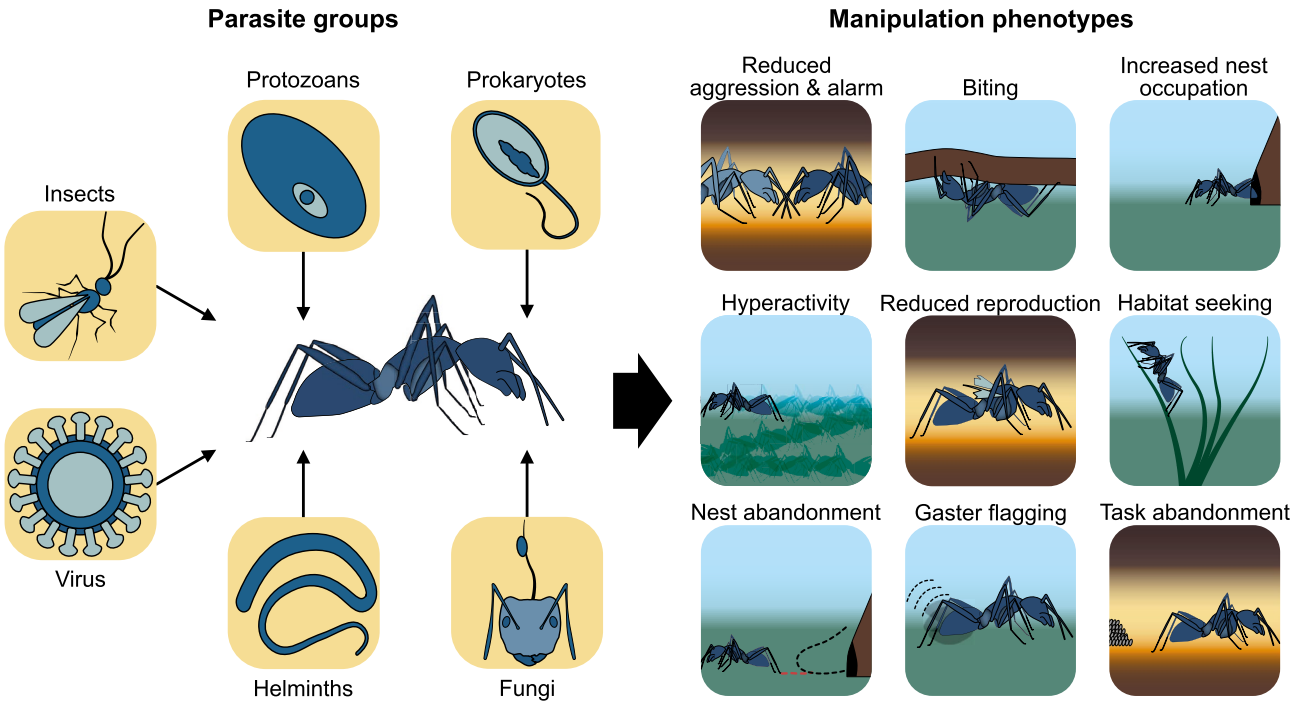

Fig. 1: Infographic depicting the various parasite groups discussed in this review and the possible parasite-adaptive behavioral modifications that one could potentially observe. For each manipulation phenotype, one of the characteristic examples, mentioned in this review, is depicted.

considered to have mutualistic relationships (Andersen & al. 2012a, Zug & Hammerstein 2015, Russell & al. 2017a). These differences in prevalence and relationships with hosts suggest a variety of fitness effects (Andersen & al. 2012a).

Wolbachia manipulate reproductive systems in certain hosts (O'Neill & al. 1997). This would benefit the (mostly) vertical transmission (i.e., through female inheritance) of *Wolbachia* as the host is modified to produce predominantly female offspring. The four kinds of observed reproductive alterations include: (a) incompatible mating (Tram & Sullivan 2002), (b) asexual reproduction (Weeks & Breeuwer 2001), (c) feminization of males (Bouchon & al. 1998), and (d) male killing (Hurst & al. 2000). A recent study on the pharaoh ant *Monomorium pharaonis* (Linnaeus, 1758) by Pontieri & al. (2017) reports a link between increased *Wolbachia* infections and a female-biased sex-ratio. Pharaoh ant workers are known to cannibalize sexual larvae, and infected colonies reared more virgin queens and fewer males. As such, *Wolbachia*-induced larval-signaling differences that predispose workers to preferentially consume male larvae have been suggested as a potential mechanism for reproductive manipulations. Yet, further experiments will be required to test for causation. *Wolbachia*-infected *Formica truncorum* Fabricius, 1804 colonies were found to produce significantly fewer sexuals (virgin queens and males) compared with healthy colonies (Wenseleers & al. 2002, Oliveira & al. 2016). The effect of *Wolbachia* in leafcutter ants has also been investigated. Infections have been found in focal species of the genus *Acromyrmex* Mayr, 1865 and *Atta* Fabricius, 1804 (i.e., *Acromyrmex echinatior* (Forel, 1899), *Acromyrmex insinuator* Schultz, Bekkevold & Boomsma, 1998, *Acromyrmex octospinosus* (Reich, 1793), *Atta cephalotus* (Linnaeus, 1758), *Atta colombica* Guerin-Meneville, 1844, *Atta sexdens* (Linnaeus, 1758), *Atta texana* (Buckley, 1860)) (Van Borm & al. 2001). How these and other *Wolbachia* infections affect sex allocation in ant colonies and how infections might affect individual, caste, and colony behavior is, however, still poorly understood. Investigating if differences in *Wolbachia* prevalence between colonies and their castes correlate with variations in sex ratios and behaviors could thus be a worthwhile avenue of research.

Spiroplasma spp. are found widely in insects, including ants. However, these reproductive manipulators are generally present at low levels compared with *Wolbachia* strains. (Russell & al. 2012). In certain cases, mutualistic *Spiroplasma* have been found to increase fitness in insect hosts such as protection against nematodes (Jaenike & al. 2010) and parasitoid wasps (Oliver & al. 2003, Xie & al. 2014) as well as enhanced overwintering abilities (Ebbert & Nault 1994). In contrast, *Spiroplasma* also have been found to induce increased host mortality (Bove 1997) and reproductive manipulation, especially male killing as seen in butterflies (Jiggins & al. 2000), ladybird beetles (Tinsley & Majerus 2006), and *Drosophila* Fallén, 1823 flies (Kageyama & al. 2007). Even though a basic understanding of the molecular mechanism underlying male killing is available (Hurst & Jiggins 2000, Ma & al. 2014), no unequivocal evidence for *Spiroplasma*-induced male killing has been found in ants yet. Some studies suggest a

mutualistic relationship between *Spiroplasma* and their ant hosts (Funaro & al. 2011, Kautz & al. 2013, Ballinger & al. 2018). However, the pyrosequencing work of Kautz & al. (2013) indicated a potential pathogenic role for *Spiroplasma* in ants. Given the ubiquity of *Spiroplasma* infections in ants, further studies to detect functionality of the apparently facultatively mutualistic and parasitic symbioses could be a very rewarding frontier.

In ants, social communication is primarily pheromone-mediated (Morgan 2009) and a plausible entryway for bacteria to modify host behavior. The proper detection of the numerous chemical communication signals among colony members requires individual ants to possess specialized odorant receptor neurons (de Bruyne & Baker 2008, Sharma & al. 2015). If the genes that encode for these receptors are experimentally altered, social communication is affected, which in turn changes task allocation and results in the disruption of social organization (Yan & al. 2017). Additionally, there is growing evidence that the host's microbiome can modulate the chemical profile and olfactory responses of that host, thus influencing their social behavior (Vuong & al. 2017, Engl & Kaltenpoth 2018). Hijacking the social communication of the host could be adaptive to the bacterial symbiont if such changes increase transmission. In fact, such bacteria-mediated altered social communication has been observed in *Drosophila melanogaster* Meigen, 1830. Flies infected with *Pseudomonas entomophila* Mulet & al., 2012, *Serratia marascens* Bizio, 1823, and *Erwinia carotovora* (Jones, 1901) secrete increased amounts of fly odors, including aggregation pheromones. This attracts healthy flies and increases dispersal rates toward new fruits, vegetables, and hosts (Keesey & al. 2017). A recent study by Silva-Junior & al. (2018) found that a strain of *S. marascens* produces certain pyrazines that were previously identified as trail pheromones of their host ant *Atta sexdens rubropilosa* (Forel, 1908). Ants use a special class of molecules known as volatile organic compounds (VOCs) as pheromones. Among them, pyrazines are commonly found to play a role in ant communication and alarm (Wheeler & Blum 1973, Cross & al. 1979, Morgan 2009, Showalter & al. 2010). However, microbes themselves also secrete VOCs that can have semiochemical signaling activity for insects (Davis & al. 2013), including Hymenoptera (Davis & al. 2012). In this case, it remains to be seen if the VOCs produced by *S. marascens* are being used as pheromones by their ant hosts or if it is indeed a case of semiochemical activity adaptive to the bacteria. It should be noted, however, that the genera *Serratia* and *Erwinia* are known to contain species that produce anti-microbial secretions (Wilf & Salmond 2012). Species from these two genera have been found to dominate the cuticular microbiome of arboreal ants in the genera *Allomerus* Mayr, 1878 and *Tetraponera* Smith, 1852 (see Seipke & al. 2013). Taken together, these studies point at the huge potential that certain bacteria have to influence signaling among colony members and thus adaptively hijack their chemical communication. Hence, more research focusing on semiochemicals in ants and the odors emitted in the presence of associated bacteria is greatly needed.

Fungi: Records of fungal manipulation of insect behavior can be found for entomopathogenic fungi of the divisions Ascomycota and Entomophthoromycota. While certain fungal species can infect a broad range of insects and do not induce conspicuous behavioral manipulations, others can have high species-fidelity and cause dramatic altered behaviors. Fungi of the genus *Ophiocordyceps* Petch, 1931 (Ascomycota, order: Hypocreales) are major players in tropical rainforests as they help maintain rainforest stability by regulating arthropod populations (Evans 1982). Many currently described *Ophiocordyceps* species are specialists of ants where each host ant species has its own highly specialized *Ophiocordyceps* parasite (Hughes & al. 2016, Araújo & al. 2018, Sakolrak & al. 2018). While ants of the genus *Camponotus* have been most frequently described as victims of *Ophiocordyceps*, species from other genera also serve as hosts (e.g., *Colobopsis* Mayr, 1861, *Polyrhachis* Smith, F., 1861, *Oecophylla* Smith, F., 1860, *Dolichoderus* Lund, 1831, *Cephalotes* Latreille, 1802, *Daceton* Perty, 1833, and *Paraponera* Smith, F., 1858; see Evans & Samson 1982, Evans & al. 2011, Luangsa-Ard & al. 2011, Kobmoo & al. 2012, Araújo & al. 2015, Kobmoo & al. 2015, Araújo & al. 2018). Typically, foraging ants become infected as they encounter fungal spores outside the nest. After the fungus has entered the ant, the parasite colonizes its body. Initially, the ant's behavior is unaltered, but as incubation time progresses, the forager abandons its daily tasks and remains within the nest (Andersen & al. 2009). In the final stages of infection, parasitized individuals start to spend more time outside the nest (de Bekker & al. 2014b, Solá Gracia & al. 2018). This is not an effect of social immunity, as nestmates do not appear to keep a notable distance or aggress the infected individuals (Solá Gracia & al. 2018). In laboratory experiments, the fungus appears to induce its host to leave the nest ca. 2 - 4 weeks after infection at the end of the incubation period (de Bekker & al. 2014b, de Bekker & al. 2015, Fredericksen & al. 2017, Sakolrak & al. 2018). At this stage, infected ants are frantically moving around the foraging arena (de Bekker & al. 2015). This is followed by climbing a vertical structure (in the lab) or vegetation (in the field) where the infected ant attaches itself, using its mandibles, in a final death grip. At this stage, the ant succumbs to the infection, and the fungus begins using ant tissues as a carbon source to form a stalk and fruiting body carrying infective spores (Andersen & al. 2009, de Bekker & al. 2015).

Research on *Ophiocordyceps*-manipulated ant behavior has focused on species of the tribe Camponotini Mayr, 1861. Field studies on *Colobopsis leonardi* (Emery, 1889) revealed that manipulated ants can end up in so-called graveyards, areas with high densities of dead, manipulated ants (Pontoppidan & al. 2009). Such graveyards have been confirmed for *Camponotus rufipes* (Fabricius, 1775) (Andersen & al. 2012b, Loreto & al. 2014), and *Camponotus atriceps* (Smith, F., 1858) (F.A. Andriolli, N.K. Ishikawa,

R.V. Isla, T.S. Cabral, C. de Bekker & F.B. Baccaro, unpubl.). What exactly drives infected ants to these specific spots in the forest remains unclear. Infected *C. atriceps* display positive phototactic behavior suggesting illumination may be an important factor (F.A. Andriolli, N.K. Ishikawa, R.V. Isla, T.S. Cabral, C. de Bekker & F.B. Baccaro, unpubl.). Humidity and temperature levels that benefit fungal growth and dispersal have also been suggested (Andersen & al. 2009). Field observations of *C. leonardi* also revealed that manipulated ants climb and bite around solar noon (Hughes & al. 2011). Similar synchronization of manipulated biting behavior is observed in the lab in experimentally infected *Camponotus castaneus* (Latreille, 1802) (see de Bekker & al. 2015). Such precise daily timing indicates that circadian rhythms exhibited by the fungus' and / or ant's biological clock play a role in the observed manipulation (de Bekker & al. 2014a, de Bekker & al. 2017b). Involvement of biological clock has also been suggested for baculoviruses that manipulate lepidopteran host behavior (van Houte & al. 2013). At the moment of biting, the muscles within the ant's body are heavily atrophied. In contrast, the brain tissue is not physically invaded and degraded (Hughes & al. 2011, Fredericksen & al. 2017). Instead of physical invasion, the fungus likely secretes bioactive compounds to alter the ant's behavior. Such compounds could act as agonists and antagonists that activate and deactivate pathways related to behavior (Molnár & al. 2010, de Bekker & al. 2014b, de Bekker & al. 2015, de Bekker & al. 2017a). Indeed, next-generation sequencing technology revealed that *Ophiocordyceps kimflemingiae* Araújo, Evans & Hughes, 2018 activates the expression of numerous secreted bioactive proteins and secondary metabolite pathways in *C. castaneus* workers during the final death grip stage (de Bekker & al. 2015). In addition, various odor receptors were down-regulated in infected, manipulated ants. This likely makes infected ants less receptive to social chemical cues. Biogenic amines are well-known for affecting animal behavior, including ants (Kamhi & Traniello 2013, Smith & al. 2013, Szczuka & al. 2013). Genes involved in the reception and production of biogenic amines (e.g., octopamine and dopamine) were also differentially expressed in infected versus healthy ants (de Bekker & al. 2015). Moreover, at the time of manipulation, putative *protein-tyrosine phosphatase*-encoding genes (*ptp*'s) were up-regulated in both the fungus and ant (de Bekker & al. 2015). In parallel, PTP has been found in baculoviruses that induce enhanced locomotory activity in the lepidopteran hosts they infect (see section Viruses above) (Kamita & al. 2005, van Houte & al. 2012). An increase in activity can also be observed in *Ophiocordyceps*-infected ants (de Bekker & al. 2015). These findings demonstrate that parallels between phenotypic and mechanistic parasitic influences on insect behavior likely exist.

Summiting (i.e., fixation at elevated positions) is also observed in ants and other insects infected with Entomophthorales fungi (Entomophthoromycotina). The number of ant-killing species among the Entomophthorales is still being debated. Recent reports suggest that there are at least two species, based on morphological data: *Pandora formicae* Humber & Balazy, 1989 and *Pandora myrmecophaga* (Turian & Wuest, 1969) (see Malagocka & al. 2017). These species have been exclusively found in association with the genus *Formica* Linnaeus, 1758 (e.g., *F. rufa* Linnaeus, 1761, *F. polyctena* Foerster, 1850, *F. pratensis* Retzius, 1783, and *F.* cf. *lemani* Bondroit, 1917 (see Loos-Frank & Zimmermann 1976, Balazy & Sokolowski 1977, Turian & Wuest 1977, Balazy 1993, Sosnowska & al. 2004, Boer 2008, Csata & al. 2013, Malagocka & al. 2015). Ants killed by *Pandora* Humber, 1989 have been found biting grasses and twigs in the proximity of foraging trails and nests (Loos-Frank & Zimmermann 1976, Boer 2008, Malagocka & al. 2017). Malagocka and colleagues speculate that infected *F. polyctena* ants die near the nest where humidity levels are optimal for *P. formicae* sporulation rather than inside the nest where humidity would be too low (Coenen-Stass & al. 1980, Steinkraus 2006). Similar to *Ophiocordyceps*-infected host species, *F. polyctena* foragers appear more susceptible to *Pandora* than their nestmates that fulfill tasks inside the nest (Malagocka & al. 2017). Fixation at elevated positions likely facilitates ideal spore dispersal while at the same time protecting the cadavers from nestmates that would normally dispose or remove dead ants from the nesting area (Loos-Frank & Zimmermann 1976, Boer 2008).

Colony and individual host level responses to *Pandora* infections are surprisingly similar to those of host ants infected with the distantly related fungus *Ophiocordyceps*. Rejection of infected nestmates might be expected as part of a social immune defense against parasites (Cremer & al. 2007). However, in both systems, healthy nestmates do not aggress or remove infected individuals from the nest (Boer 2008, Solá Gracia & al. 2018). Moreover, both manipulative parasites precisely time when they make their hosts leave the nest, climb the vegetation, and latch on until death. Entomophthoralean fungi, including *Pandora*, seem to time this to the late afternoon or evening (Marikovsky 1962), with an exquisitely precise synchronization of attachment reported for infected *Formica* species (Loos-Frank & Zimmermann 1976). Detailed field observations further describe how infected *Formica pratensis* and *Formica rufa* move in an uncoordinated manner. Parasitized ants continuously open and close their mandibles while summiting, before attaching themselves with the head upward. Manipulated individuals also move up and down the leaf and never return to the ground. The fungus grows rhizoids that firmly attach the ant to the substrate. Subsequently, hyphal structures with infective spores emerge from intersegmental parts of the mesosoma and gaster (Loos-Frank & Zimmermann 1976, Boer 2008). Dissections of field-collected samples showed that *Pandora* does not grow into the ant's brain tissue. This suggests that bioactive compound secretion might be the mechanism of manipulation, similarly to what is hypothesized for *Ophiocordyceps*. Verification of the mechanisms used by entomophthoralean fungi are, however, somewhat

complicated. Unlike *Ophiocordyceps*, fungal isolation and culturing is difficult, which makes experimental infections of *Formica* challenging. Transcriptomics studies on field samples revealed fungal gene expression post manipulation (Malagocka & al. 2015), but gene activation and deactivation during summiting have yet to be explored. However, the parallels with *Ophiocordyceps* infections, in which the mechanisms underlying behavioral manipulation have likely convergently evolved (Loreto & al. 2018), suggest that findings from *Ophiocordyceps*-ant infections might be homologous to those in the *Pandora*-ant systems.

Despite the many studies of *Metarhizium* Sorokin, 1883 (Ascomycota, order: Hypocreales) infecting various arthropods, these generalist fungal parasites are considered to not have any behavioral effect on their hosts. However, alterations of ant behavior upon infection have been reported for parasite-host interactions in which behavior has been studied more closely. *Metarhizium brunneum* Petch, T., 1935-infected *Myrmica rubra* (Linnaeus, 1758) ants become phototropic (Leclerc & Detrain 2017). Ultraviolet light can kill spores and heat can stimulate the innate immune system, thus infected ants attracted to light may be exhibiting an adaptive mechanism that benefits the ant (Rotem & al. 1985, Blanford & Thomas 2001, Braga & al. 2015). However, heat could also aid fungal development inside the host (Blanford & al. 1999). Additionally, *M. brunneum*-infected *M. rubra* gradually lose attraction for social cues. This results in infected individuals socially secluding themselves from nestmates and eventually leaving the nest (Leclerc & Detrain 2017). As with *Ophiocordyceps* and *Pandora* infections, no aggression was observed against *M. brunneum*-infected individuals. Similar observations have been made for other generalist fungi (Bos & al. 2012, Leclerc & Detrain 2016). Such behavior limits exposure of conspecifics to the parasite (Cremer & al. 2007). Therefore, leaving the nest upon infection might be a behavior that is adaptive to the host ant, while it is assumed to be adaptive to the parasite in summit-inducing fungi (see above). The question who the true benefactor of this behavior is (maybe it is adaptive to both!) begs further detailed experimentation.

Ectoparasitic fungi have also been observed infecting ants, regularly with unknown consequences (Adams & al. 2012). Ectoparasite *Rickia wasmannii* Cavara, F., 1899 (Ascomycota, order: Laboulbeniales) is an obligatory parasite of ants of the genus *Myrmica* Latreille, 1804, with the majority of infections found in *Myrmica scabrinodis* Nylander, 1846. The fungal thalli on the outer layer of the cuticle make infected ants look unusually hairy. While the fungus can spread to nestmates, older individuals of the foraging caste are predominantly infected (Markó & al. 2016). Behavioral response to infected individuals at the colony level have been observed. Allogrooming frequency increases drastically in infected nests (Csata & al. 2014). Moreover, infected workers display reduced aggression towards non-nestmates and unrelated queens. This makes polygyny in *Rickia*-infected colonies much more likely. Parasitic butterfly larvae also have a higher chance to be accepted into the colony (Csata & al. 2017). This might be due to increased heterogeneity of the colony's cuticular hydrocarbon (CHC) *gestalt* odor (vander Meer & al. 1998, Barbero 2016), which is used by workers to assess an ant's chemical profile and recognize nestmates. *Rickia wasmanii* changes the relative concentrations of its host's CHC (Csata & al. 2017), which results in a more flexible margin of error in infected *M. scabrinodis* colonies. The similarity threshold used to distinguish nestmates from parasites and non-nestmates likely also becomes less stringent. The fungal parasite thus appears to shape associations of *Myrmica* with other organisms. *Myrmica* ants interact with a variety of invertebrates and myrmecophilic parasites (Witek & al. 2014). Such fungal influence on their behavior could therefore have rather large ecological consequences (Csata & al. 2017).

Great strides have been made towards unraveling how certain fungal parasites manipulate ant host behavior. However, much more detailed work is needed to truly uncover the mechanisms. Even though transcriptomics studies have been performed on certain species interactions, the returned candidate-gene list is long and not definitive. Follow-up functional studies and comparative transcriptomics studies on other, related species interactions could help narrow down the key components. This is an especially exciting endeavor because of the parallels that exist between the behavioral changes induced by highly unrelated fungal species, viruses, trematodes, and Strepsiptera (e.g., summiting, biting, wandering, phototaxis, daily timing; see sections Viruses, Helminths as well as Insect parasites). As the discoveries of *ptp* homologs in virus-Lepidoptera and *Ophiocordyceps*-ant systems suggest, unraveling the underlying mechanism in one system could inform us about the mechanisms of others as well.

Protozoans: The few protozoans of insects that have been described have been reported to appear relatively harmless, having little to no effect on their hosts (Schmid-Hempel 1998). However, this could be due to our limited understanding of their biology and natural history. The reports on protozoan symbionts of ants are minimal and are generally discussed in the context of biological pesticide use against fire ants (Williams & al. 2003). They either reside among the apicomplexan gregarines, or within the Microsporidia, which is currently recognized as a fungal phylum rather than protozoan (Hibbett & al. 2007). Only a few microsporidian parasite species of ants have been described to date. All were discovered within the context of their potential use as biocontrol agents without the reporting of any behavioral impacts (Oi & Valles 2009, Plowes & al. 2015). Gregarines have been found to affect the foraging behavior of the social wasp *Polybia occidentalis* (Olivier, 1791) by lowering foraging rates in infected adults. As a consequence, adult mortality rates dropped in infected colonies, as did overall colony productivity (Bouwma & al. 2005). For fire ant species infected with *Mattesia* Naville, 1930, no effect on colony or individual behavior has been reported. *Mattesia* infects the hypo-

dermis of larval stages. This results in disruption of eye development and cuticle melanization, followed by death (Jouvenaz & Anthony 1979, Jouvenaz 1983). In the primitive Australian ant *Myrmecia pilosula* Smith, F., 1858, larvae are also infected by gregarines. Here, infected larvae do eclose, resulting in adults with conspicuous, brown (instead of black) cuticles (Crosland 1988). It is not known if this color alteration has adaptive function. Due to the fact that protozoan-ant interactions are largely unexplored, it is difficult to determine if investigation into the possible behavioral influences of protozoans on ants is a worthwhile endeavor. However, the sheer absence of knowledge about this group of parasites – and the ants that they might infect – is a knowledge gap that is ready for the taking.

Helminths: Helminths include some of the most striking cases of macroparasite-induced alterations of host behavior. A quintessential example is the trematode *Dicrocoelium dendriticum* (Rudolphi, 1819) (Dicrocoeliidae), which induces a biting behavior and convulsions in ants on the tips of vegetation. This summiting behavior facilitates trophic transmission by exposing manipulated individuals to the parasite's definitive grazing-mammal hosts (e.g., sheep) (Hohorst & Graefe 1961, Manga-González & al. 2001). Infection has most commonly been found and studied in *Formica* species such as *F. fusca* Linnaeus, 1758, *F. polyctena*, *F. pratensis*, *F. rufa*, and *F. rufibarbis* Fabricius, 1793 (see Hohorst & Graefe 1961, Lucius & al. 1980, Paraschivescu & Micev 1980, Romig & al. 1980, Spindler & al. 1986, Moore 1995, Manga-González & al. 2001, Botnevik & al. 2016). Manipulated biting is coordinated with changes in temperature and follows a daily rhythm between the evening and morning hours. Outside this period, the trematode loosens its grasp on the host and the ant leaves the plant to presumably return to normal activity (Manga-González & al. 2001, Botnevik & al. 2016). The timing of manipulated biting and placement at the tips of vegetation appear to be stereotypic constants. Such constants in placement and timing have also been observed in fungus-infected ants, for instance (see section Fungi). However, no rigorous selection of vegetation type or fidelity to a precise biting location over successive days has been observed (Paraschivescu & Micev 1980). Biting and tetany appear tightly, and solely, tied to temperature (Botnevik & al. 2016). Temperature might influence the expression of biting behavior to align tetany with definitive host availability. Physiological effects of temperature on the ability of the parasite to dysregulate host behavior have also been suggested. Additionally, operating within precise temperatures might avoid risk of death due to temperatures outside of the ant's or trematode's tolerable range (Manga-González & González-Lanza 2005, Botnevik & al. 2016).

The precise mechanisms that underlie *Dicrocoelium dendriticum* manipulation of ant behavior have yet to be fully described. However, elements of the parasite's natural history inform hypotheses about possible mechanisms. Ants are infected by ingestion of free-living larvae (i.e., cercariae) released by intermediate snail hosts. Upon infection, a single cercaria settles within the suboesophageal ganglion of the ant's brain, in close association to the mandibular nerve. The other ingested cercariae develop into metacercariae elsewhere in the body of the host. Although the "brainworm" cercaria does not encyst and develop further, it is thought to be critical in inducing the altered behavior of parasitized ants (Manga-González & al. 2001, Mehlhorn 2015). Whether the parasite acts by chemical secretion, tissue destruction and impingement, or other means is currently unknown.

Other trematodes appear to drive similar behavioral changes in ants. *Dicrocoelium hospes* Looss, 1907 infects *Camponotus compressiscapus* André, 1889 and causes infected ants to sit at elevated, exposed sites in a manner similar to *Dicrocoelium dendriticum*. These ants, however, do not display the characteristic biting behavior and temperature coordination as observed in *D. dendriticum* (see Romig & al. 1980). *Dicrocoelium hospes*-infected ants showed reduced startle responses to changes in light, temperature, and humidity (Lucius & al. 1980). While *D. dendriticum* infects multiple *Formica* species, *D. hospes* has only been observed in *C. compressicapus* (see Lucius & al. 1980). Additionally, infections typically include two brainworms; one located in each antennal lobe (Romig & al. 1980, Mehlhorn 2015). Infections by *Brachylecithum mosquensis* (Skrjabin & Isaitschikoff, 1927) of *Camponotus herculeanus* (Linnaeus, 1758) and *Camponotus pennsylvanicus* (De Geer, 1773) also cause ants to linger at exposed locations and have reduced activity and responsiveness (Carney 1969). This parasite similarly infects the ant brain, but, again, in a stereotypically different position; *B. mosquensis* brainworms inhabit the supraesophageal ganglion.

The shared and unique elements among the natural history of these trematodes offer a significant opportunity for researchers to perform comparative studies and unravel mechanisms of host manipulation. The summiting phenotype in a range of ant hosts may be established in similar fashion. The brainworms of each parasite are intimately placed in the ant's central nervous system and could be secreting similar neuromodulatory compounds. Such compounds might be homologous to those secreted by fungi that induce similar summiting behavior in ants (see section Fungi) or viruses that induce climbing in lepidopteran larvae (see section Viruses). Yet, there are also differences in the manipulated phenotypes. The biting by *D. dendriticum* hosts may be connected to the unique placement of the brainworm in this interaction. One may speculate that the specific location of *D. dendriticum* near the mandibular nerve suggests a physical interaction to elicit biting. Alternatively, the key may lie in differences among the ant hosts. They might vary in susceptibility and response to similar parasite mechanisms. Deeper investigations of possible mechanisms, for instance by ways of comparative transcriptomics, would add critical knowledge to interpreting the biology of these fascinating trematode-ant interactions.

Host modifications can also include concomitant morphological changes. *Cephalotes atratus* (Linnaeus, 1758) ants infected by *Myrmeconema neotropicum* Poinar & Yanoviak, 2008 (Tetradonematidae) nematodes develop a conspicuous, berry-like gaster. This modification is hypothesized to attract birds to feed on modified ants (Yanoviak & al. 2008). Ant larvae, fed nematode-contaminated food, suffer reduced growth with further behavioral and morphological changes in adulthood (Yanoviak & al. 2008). Gravid with nematode eggs, their gaster appears bright red and berry-like and has a weakened gaster-postpetiole junction (Yanoviak & al. 2008). These modifications would advertise the gaster as ripe fruit to attract frugivorous host-birds and allow ease of detachment of the egg-laden gaster from the ant's body (Hughes & al. 2008, Yanoviak & al. 2008). Furthermore, the morphological changes are accompanied by deviations from typical *C. atratus* behavior. Infected ants display gaster-flagging behavior, making the berry-like gaster even more conspicuous to foraging birds. Reduced activity and alarm responses also coincide with progressively developed parasite burdens (Poinar & Yanoviak 2008, Yanoviak & al. 2008). Taken together, such modifications plausibly create a visible, attractive, and easy-to-capture meal for passing birds to promote nematode transmission.

Researchers have begun to test hypotheses and reveal possible mechanisms underlying the observed changes in *C. atratus*. *Myrmeconema neotropicum* achieves the fruit mimicry, at least in part, by thinning the walls of the gaster and the production of yellowish eggs. Cuticular thinning is fairly constrained to the gaster area and appears to be well controlled to produce a stereotypic thickness. This suggests that the parasite is regulating the degree of thinning, perhaps by incorporating cues such as incoming light (Verble & al. 2012). Whether other mechanisms, such as altered melanin levels, act in concert has not yet been explored. Yanoviak & al. (2008) also noted that parasites do not damage host tissues in the gaster haphazardly. Only the ventral nerve cord showed signs of distress and injury. If, and how, this may be related to the observed manipulated phenotype has not yet been shown. Gaster-flagging behavior by infected *C. atratus* is not a simple response to the host's large and unwieldy load of parasites. Adding weight to the gasters of healthy ants to mimic a parasitized gaster changed their gait but did not invoke gaster flagging (Yanoviak & al. 2008). Flagging behavior is thus quite possibly a true manipulation. The precise drivers of host lethargy are yet to be understood. However, the important step of using quantitative approaches to attempt to contrast metabolic rates of healthy ants and those harboring *M. neotropicum* have been taken (Shik & al. 2011).

Shifts in host behavior can also be less dramatic. This complicates the differentiation between parasite-adaptive manipulation, host-adaptive responses, and a specific disease symptom. *Anomotaenia brevis* (Clerc, 1902) (Dilepididae) cestodes infecting *Temnothorax nylanderi* (Foerster, 1850) ants present a subtle case of behavior changes in the individual worker. Additionally, they offer an interesting example of possibly colony-wide manipulation of uninfected individuals. This raises the point that manipulation may operate at multiple scales in eusocial superorganisms such as ants (Hughes & al. 2012). At the single-ant level, infected larvae develop into smaller, yellow adults that show reduced escape responses and lower aggression toward conspecifics. They spend more time inside the nest, display less activity of colony duties, and live longer (Moore 1995, Beros & al. 2015). Infected individuals also appear well cared for and tolerated. This leaves the parasites in a cozy position until the colony is attacked by a predating woodpecker. The slow-to-flee infected individuals are easy targets, increasing trophic transmission of the parasite to the bird. The possible manipulation has been reported to extend beyond the single worker by reducing whole colony aggression against conspecifics (Scharf & al. 2012, Beros & al. 2015). Relaxation of colony CHC identity by sharing of atypical parasitized ant CHC profiles have been hypothesized to underlie reduced aggression (Trabalon & al. 2000, Beros & al. 2015). Similar effects from changes in colony CHC and *gestalt* odor have been observed in the fungal parasite *Rickia wasmannii* (see section Fungi). However, Beros & al. (2017) propose that the presence of infected nestmates does not drive colony-wide CHC shifts and suspect other mechanisms to reduce aggression.

Gene expression in brains of *A. brevis*-infected ants correlate with changes in host infection status (Feldmeyer & al. 2016). Comparing ants under different parasite pressures returned differentially expressed genes among infected ants, their nestmates, and unexposed controls from parasite-free colonies. Genes reported include ones possibly linked to muscular atrophy and longevity. Such candidates align well with a story of feeble, long-lived hosts. Moreover, Feldmeyer & al. (2016) report the finding of a putative gene that is related to aggression in *Drosophila*. They propose this gene to be involved in mediating the reported changes in aggression in uninfected nestmates. These efforts are a start to uncover the mechanisms underlying the subtle host changes. They should, however, be followed by further examinations. Functionally testing candidate genes proposed to underscore changes in host behavior would be a critical next step.

Enhanced trophic transmission is not the only result of helminth-driven behavior. Infection by nematodes of the genus *Mermis* Dujardin, 1842 (Mermithidae) has been observed to drive a water-seeking behavior in *Colobopsis* Mayr, 1861 ants. This allows the parasite to emerge from the host in an environment that is necessary for its reproduction (Maeyama & al. 1994). *Pheromermis villosa* Kaiser, 1986 is implicated in a very similar behavior in ants of *Lasius flavus* (Fabricius, 1782) and *Lasius niger* (Linnaeus, 1758) (Kaiser 1986). Parasitized ants displayed great determination in reaching water, even if repeatedly removed by experimenters. Poinar & al. (2007) demonstrated that *Allomermis solenopsis* Poinar, 2007 nematodes, infecting the fire ant *Solenopsis invicta*, depend on standing water for emergence from their hosts.

The authors go on to suggest water seeking as a plausible strategy to improve the parasite's chances of reaching this necessary water. *Mermis* infections have additionally been shown to be associated with less dramatic behavioral and morphological changes such as reduced colony activities and aggression, increased photophobic responses, higher trophallaxis demands, and developmental changes in head width, limb length, wing size, and coloration (Wheeler 1928, Laciny & al. 2017). These perhaps more general shifts in host behavior are hard to interpret without clear analyses of fitness outcomes and driving mechanisms.

Crickets infected with analogous nematomorph hairworms can be major players in their ecosystem, with the manipulated host acting as a novel and abundant food source for aquatic organisms (Sato & al. 2011a, b). Given the substantial biomass of ants in many communities, nematode-manipulated individuals may also be playing a notably different ecological role from their healthy conspecifics. Moreover, the exploration of the molecular underpinnings in the cricket-hairworm system using proteomics tools (Biron & al. 2005a) can serve as an inspiration to those who wish to investigate the proximate mechanisms underlying nematode-induced manipulation of ant host behavior.

Insect parasites: Ants are also attractive hosts to other insects. Studies frequently focus on flies, but parasitoid wasps and "twisted-wing" parasites have also been reported, in addition to socially parasitic ants and various myrmecophilic insects. These insect parasites attack individuals or invade host colonies.

A considerable number of parasitoid wasp species that afflict ants have been documented (Pérez-Lachaud & al. 2012 and references therein), with many more cryptic species likely to be revealed with wide-scale barcoding efforts (Smith & al. 2008, Hall & al. 2017). Most parasitoid wasps consume host larvae or pupae and gain access to the nest in a variety of ways. Some wasp larvae are transported to the host nest by worker ants (i.e., phoretic attachment) during early developmental stages (e.g., *Orasema* Cameron, 1884 spp. parasitizing *Camponotus* spp.) (Herreid & Heraty 2017). Other wasp species likely enter the host nest to lay an egg directly into the host brood or attack brood as it is being transported (e.g., *Hybrizon buccatus* (Brebisson, 1825) parasitizing *Lasius grandis* Forel, 1909) (see Durán & Achterberg 2011). The infected hosts are sheltered in the protective ant nest, shielding the developing wasp from predators and pathogens (Feener 2000). This obscures the detection of possible behavioral manipulation caused by parasitoids that infect ants in the larval and pupal stage. Infected larvae could be manipulated to solicit food more frequently from the ant workers if larvae are young and still feeding. Additionally, the parasitoids might elicit a response in adult workers to spend more time and energy grooming infected individuals. Research questions asking how brood-infecting parasitoids might affect ant behavior, if at all, and how this would impact colony fitness, would, to our knowledge, be a novel field of study.

Within the parasitoid wasp family Braconidae, there are several known species from the tribe Neoneurini Bengtsson, 1918 that attack adult ants (Durán & Achterberg 2011). Extant genera include *Elasmosoma* Ruthe, 1858, *Kollasmosoma* van Achterberg & Argaman, 1993, and *Neoneurus* Haliday, 1838. *Elasmosoma* associate with the Formicine genera *Lasius* Fabricius, 1804, *Camponotus*, and *Formica,* the latter being the most common (Durán & Achterberg 2011). *Elasmosoma michaeli* Shaw, 2007 wasps cause colony-level distress in *Formica obscuriventris* Mayr, 1940 while hovering above the ants before oviposition (Poinar 2004). The ants have been observed responding violently, attempting to catch the wasps in the air. Similar oviposition behavior is recorded for *Elasmosoma luxemburgense* Wasmann, 1909 on *Formica rufibarbis* (see Durán & Achterberg 2011). Both parasitoid species lay their eggs in the ant's gaster. After oviposition by the wasp, the parasitized ants are visibly agitated but eventually resume normal duties. When *E. michaeli* is in the late third instar stage, infected *F. obscuriventris clivia* ants appear to be manipulated by the wasp. They show reduced aggression, abandon their tasks, and assemble in groups just outside the nest to receive food from returning foragers after which they either go back into the nest or wander off. Poinar (2004) speculates that such nest abandonment may be an indicator of parasite readiness to emerge. Just before pupation, the wasp exits the ant gaster through the anus leaving the ant dead or dying. Interestingly, the larva is not attacked by uninfected host ants and is left to make a small impression in the soil and start spinning a cocoon (Poinar 2004). Despite having the wasp larvae consuming the contents of the gaster, parasitized individuals appear to perform tasks that benefit the colony for most of their lives, lessening the parasitoid's impact on the colony (Poinar 2004). Such a low impact on colony fitness could explain why the ants have not evolved to attack emerging wasp larvae. The mechanisms responsible for the solicitation of food and wandering behavior by the host ants are currently unknown. This parasite-host interaction is, however, tractable from initial infection all the way to manipulation and wasp emergence. Such tractability makes transcriptomics studies to investigate the gene expression of wasp larvae and ant hosts up to the late third instar phase feasible. This will give a mechanistic insight into the subtle behavioral changes observed and might encourage more research on the behavior of the ants and their wasp parasitoids, which is currently severely lacking.

Unlike hymenopteran parasitoids that only parasitize arthropods, dipteran parasitoids have a wide range of hosts from five phyla, including social insects (Feener & Brown 1997 and references therein). The Phoridae, Chloropidae, Syrphidae, and Tachinidae contain species that attack ants (Gösswald 1950, Hölldobler & Wilson 1990, Feener 2000). There are a diversity of known ant-associated genera among the Phoridae, such as *Pseudacteon* Coquillett, 1907 (see Patrock & al. 2009, Morrison 2012), *Apocephalus* Coquillett, 1901 (see Brown &

Feener 1991), *Eibesfeldtphora* Disney, 1996 (see Brown 2001, Disney & al. 2009), *Myrmosicarius* Borgmeier, 1928 (Disney & al. 2006), and *Neodohrniphora* Malloch, 1914 (see Disney & al. 2009, Pérez-Lachaud & al. 2017). These have been found to parasitize ants in the genera *Solenopsis, Plagiolepis* Mayr, 1861, *Atta*, *Acromyrmex*, *Formica*, *Pheidole* Westwood, 1839, *Pachycondyla*, and *Linepithema* Mayr, 1866 (see Hölldobler & Wilson 1990 and references therein). With the exception of species from *Apocephalus* and *Ceratoconus* that attack brood, flies most often target workers with a range of oviposition sites (e.g., head, thorax, gaster) (Porter & al. 1995, Tonhasca & al. 2001, Bragança & al. 2002, Brown & al. 2017, Pérez-Lachaud & al. 2017).

Colony-level distress is obvious when flies are present and threatening. As the flies hover over foragers, the ants will contort their bodies to limit oviposition sites or violently snap at the flies with their mandibles (Cônsoli & al. 2001). Dipteran parasitoids can also have significant ecological implications for the host species, affecting foraging patterns spatially and temporally as well as changing dominance hierarchies in ant communities (Mehdiabadi & Gilbert 2002, LeBrun 2005, LeBrun & Feener 2007). Such behavioral changes have been observed in fire ant colonies that face phorid threats and result in negative fitness consequences for the host. These behaviors are, however, considered to be host-behavioral responses to the parasite, rather than host manipulations that benefit the parasitoid. Much parasitoid research is focused on identifying potential fly species with host specificity and colony-level impact to determine if a biocontrol effort is feasible (Guillade & Folgarait 2011, Guillade & Folgarait 2014). As such, research on fire ant parasitoids has advanced considerably because of the *S. invicta* threat in North America (Jetter & al. 2008).

Pseudacteon parasitoid fly species have already been tested as biological controls against fire ants. However, their impact at the colony level is not yet clear (Cônsoli & al. 2001, Oi & al. 2015 and references therein). Of the *Pseudacteon* genus, a substantial number of parasitoid species have been associated with the *Solenopsis saevissima* and *Solenopsis geminata* (Fabricius, 1804) species groups (Patrock & al. 2009, Plowes & al. 2009). However, most research has focused on the red imported fire ant, *Solenopsis invicta*, a member of the former group. *Pseudacteon* species are conveniently referred to as the decapitating flies because their final developmental stages take place in the host ant head, causing it to fall off (Porter & al. 1995). *Pseudacteon tricuspis* Borgmeier, 1925 attacks *S. invicta* by injecting an egg into the thorax where the developing larvae will increase 100-fold in volume as it consumes the ant's hemolymph (Cônsoli & al. 2001, Tschinkel 2006). After an egg has been laid, the victim ant freezes, is groomed by her sister workers, then apparently continues performing tasks as usual (Tschinkel 2006). The young elongate *P. tricuspis* larvae molt as they migrate from the thorax towards the head where they remain for the second and third instar. During this last instar, the ant acts noticeably different as the maggot consumes the content of her head capsule leaving the brain for last. As this ant leaves the nest, an enzyme is secreted by either the fly or the ant that softens the intersegmental membrane between the head and thorax causing the head to fall off. Then the maggot pupariates inside the head capsule outside of the host nest.

Besides when ants are visibly disturbed and distracted from their foraging efforts by hovering phorids, parasitized ant behavior is manipulated by the flies albeit in subtle ways. Henne & Johnson (2007) conducted an observational laboratory study and found that fire ants infected by *Pseudacteon tricuspis* largely remain in the nest until ca. 8 - 10 hours before host decapitation. This behavior occurs in host ants regardless of the developmental success of the parasitoid. Accessory gland openings in young phorids were not observed, nor did preliminary work with cultured larvae detect larvae-derived chemicals. These observations suggest chemicals that influence this behavioral change may be injected by the fly with the egg (Cônsoli & al. 2001). Parasitized individuals tend brood and remain near the brood pile but are less aggressive than non-parasitized individuals are. Still, infected ants will expel venom and attempt to escape when being handled with forceps (Henne & Johnson 2007). The cessation of foraging behavior and the maintenance of personal defense directly benefits the survival of the developing parasitoid. Therefore, Fritz (1982) proposed a hypothesis that parasitoids alter the behavior of host ants to ensure personal survival. In other words, behavioral manipulation ensures that the ant remains in microclimatic conditions that are ideal for parasitoid development and additionally protect the parasitoid inside the host ant from predators and possible hyperparasites. In a laboratory experiment, infected ants that left the nest moved into sand, soil, and sod thatch layers burying themselves despite their limited ability to move their mandibles (Henne & Johnson 2007). The results suggest that during the late stages of their larval development, phorid flies may influence searching and digging behavior of the host ant. Furthermore, leaving the host colony before the flies emerge from the head should reduce the possibility of attack by uninfected nestmates. Interestingly, similar "nest desertion" behavior has been reported in honeybees parasitized by the phorid *Apocephalus borealis* (see Core & al. 2012).

The extent to which the altered behavior of phorid-infected fire ants affects colony fitness is not yet well understood. Moreover, the exact mechanisms that phorids employ to manipulate the host as to further their own life cycle has not been identified either. There are several established labs breeding and releasing phorids for biological control providing great opportunities to study interactions between the hosts and parasitoids. In the cases where the parasitoids attack adult ants, host behavior manipulation is a plausible element of the infected phenotype. Such manipulation could involve reduced foraging and aggression behavior, followed by the infected ant straying from the nest to allow the phorid larva to emerge and

finish its life cycle without risking attack by nestmates. Because fly parasitoids lack venom and the associated accessory glands, physiological and potential behavioral manipulation is likely achieved by different mechanisms than wasp parasitoids (Feener & Brown 1997). Comparative transcriptomics methods that explore and compare gene expression across fire ant-phorid species interactions could reveal common mechanisms underlying the changed behaviors observed.

The order Strepsiptera contains several hundreds of known species of "twisted wing parasites" that infect a variety of insect orders across a worldwide distribution. The Myrmecolacidae, are the only family of strepsipterans that are known to attack ants (Kathirithamby 2009). Myrmecolacids are most often reported to parasitize Formicinae and Myrmicinae, but have also been observed in Dolichoderinae, Ecitoninae, Ponerinae, and Pseudomyrmecinae (Hughes & al. 2003, Kathirithamby 2009). Intriguingly, only male myrmecolacids parasitize ants; the females infect mantids or orthopterans, such as crickets. The obligate parasitism of different host orders by the two sexes of the parasitoid appears nearly unique, with other examples currently only documented in the family Aphelinidae (Kathirithamby 2009). In addition to differing host use, the life cycles and morphology of male and female myrmecolacids are strikingly dimorphic. The Myrmecolacidae, and most other strepsipterans, have ephemeral, free-living adult males. Females retain larva-like morphology into adulthood, are long-lived, and remain endoparasitic. Once the short-lived adult male parasite emerges from his ant host, he has only hours to seek females residing within their still-living host (Kathirithamby 2009). The female keeps her head subtly exposed between the abdominal segments of the host, but otherwise remains fully within and hidden. Her head contains a brood canal for insemination and for release of larvae. Pheromone cues released by the otherwise cryptic female assist the male in locating a mating partner (Cook 2014). She then live-births first-instar larvae that invade new orthopteran or mantid nymphs and infect ant brood presumably via phoretic transport on foraging workers (Kathirithamby 2009). The emergence of either the adult male or the release of larvae are sufficiently traumatic that the host typically dies shortly after due to injury and opportunistic infections. However, until this time, infected hosts continue to develop and may even out-live their conspecifics as they are castrated by the parasite but not otherwise significantly damaged (Kathirithamby 2009). Myrmecolacidae sex determination and acquisition of sex-specific hosts remains unclear. Three main possibilities have been proposed: environmental sex determination after infection, sexually dimorphic host seeking behavior, or production of numerous offspring to overcome mismatches from untargeted infection attempts (Kathirithamby 2009, Cook 2014).

Initial observations of *Neoponera apicalis* (Latreille, 1802) and *Neoponera verenae* Forel, 1922 ants parasitized by male *Myrmecolax incautus* Oliveira & Kogan, 1959 indicate two stages of behavioral changes in infected ants. First, once the male parasite extrudes its head through the infected ant's abdomen and begins to pupate, the host becomes more lethargic, abandons tasks, and remains in the nest more often. Then, shortly before emergence of the parasite, the ant becomes increasingly active, running along vegetation to an elevated position (Kathirithamby & al. 2010). Similarly, parasitized *Solenopsis* become positively phototactic and summit to a raised location (Cook 2014). Cook (2014) additionally notes that Ogloblin (1939) was only successful in collecting parasitized ants by sweeping tall grass at midday – a location and time outside normal host activity. We discuss summit disease and enhanced locomotion activity as extended phenotypes of manipulating parasites in this review (see sections Viruses, Fungi, as well as Helminths), and these manipulations appear to be in play with myrmecolacid infection as well. Such changes in behavior could plausibly facilitate dispersal and mate seeking by the parasite.

A well-studied example of strepsipteran influences on a hymenopteran host is the primitively eusocial paper wasp *Polistes dominula* (Christ, 1791) parasitized by the strepsipteran *Xenos vesparum* Rossi, 1793 (Family: Xenidae). Healthy *P. dominula* gynes aggregate when overwintering. However, parasitism by *X. vesparum* would induce the early formation of inactive, multi-colony aggregates that include workers (Hughes & al. 2004, Geffre & al. 2017). Hughes & al. (2004) suggest that the observed aggregations may play a role in allowing the short-lived males to locate females, and hence be a case of parasite-adaptive manipulation. Induction of aberrant aggregation behavior in worker wasps is correlated with changes in host gene expression profiles, shifting infected workers to a more gyne-like pattern (Geffre & al. 2017). Furthermore, infected wasps are castrated by the parasite and display reduced activity and aggression. According to Dapporto & al. (2007) the reduction of juvenile hormone, as a result of castration, possibly underlies this altered behavior. Subsequently, during the nesting season after winter, host wasps carrying female parasites visit multiple nesting sites, allowing infectious parasite larvae to escape and invade new hosts (Beani & Massolo 2007).

Ants hold a unique place in the biology of Strepsiptera as the obligate host for male myrmecolacid strepsipterans, and in turn may be subjected to manipulations to meet the demands of the male parasite's short life. The work in paper wasps offers inspiration for myrmecologists, illustrating how one strepsipteran interacts with its eusocial hymenopteran host. The combination of behavioral observations and molecular techniques could reveal underlying mechanisms that can and should be applied to ants. Myrmecolacidae species have been notoriously difficult to positively identify and study due to their cryptic endoparasitic lifestyle, sexually dimorphic host use, and nondescript females. However, current molecular approaches equip researchers with the tools to delimit species and begin investigating these parasites and the effects on their hosts (Kathirithamby & al. 2010).

A variety of parasitic ants use chemical signals to deter, confuse, and fool hosts. Social parasitism, defined as the coexistence of two social insects in the same nest where one is parasitically dependent on the other, is widespread among social Hymenoptera (Hölldobler & Wilson 1990). Social parasites and myrmecophiles, organisms that live at least some part of their life inside ant nests (Hölldobler & Wilson 1990), take advantage of the social structure and communication systems of social insect colonies. There are varieties of ant nest associates that have converged on similar infiltration strategies that allow them to enter the protected host nest. Some use "propaganda" chemicals and weaponry to gain access to the host colony (Allies & al. 1986, Martin & al. 2007, Neupert & al. 2018) while others alter (Cristina Lorenzi & al. 2011, Włodarczyk & Szczepaniak 2017), acquire (D'Ettorre & al. 2002, Kather & al. 2015), mimic (Akino & al. 1999), or have muted CHC profiles (Neupert & al. 2018). Cuticular hydrocarbons are used as nestmate recognition signals (e.g., chemical passwords), and a variety of ant-nest invaders take advantage of this system and fool their host colony into thinking they are kin (Guillem & al. 2014). Once inside, the intruders have access to shelter and the stored resources of a colony (e.g., brood and food). They may even solicit food directly from the unsuspecting host ants. In addition to being fed, they may also be groomed and tended by the host ants (Adams & al. 2012). The numerous examples of myrmecophilic parasites and the mechanisms they employ to induce behavioral changes in their hosts (e.g., chemical trickery) are reviewed by others and are beyond the scope of this review (Lenoir & al. 2001, Akino 2008, Cushing 2012, Parker 2016).

Here, we focus on the understudied special case of castration by social parasites. Castration is an act that forces a redirection of energetic expenditure by the host (Baudoin 1975) where they shift resources once allocated for reproduction to growth and / or maintenance (Forbes 1993). A broad range of parasite taxa castrate their hosts, which is predicted to have an adaptive significance that benefits the parasite (Baudoin 1975, Lafferty & Kuris 2009). Host castration can be caused by the direct destruction of gonadal tissues (i.e., parasite consumes or lives within host gonads) or indirect alteration of secondary sexual characters and / or gonads (Noble & Noble 1971). Some social parasites enter the nest and castrate the colony by killing the host queen (the sole reproductive). The parasite then takes over the reproductive duties and uses the newly acquired worker force and energy stores to boost colony growth early in her life cycle (Wheeler 1910, Buschinger 2009). This indirect behavioral manipulation of host worker labor – gained through chemical trickery and elimination of the queen – presents a less physiologically invasive form of host manipulation as discussed in other sections of this review.

A perhaps more comparable type of castration is when parasites attack host gynes (virgin queens) forcing them to stay in their natal nest and forgo their nuptial flight and subsequent dispersal (Adams & al. 2012). *Trachymyrmex* cf. *zeteki* Weber, 1940 gynes are castrated via wing clipping by guest ant parasites, *Megalomyrmex adamsae* Longino, 2010. This is an example of the modification of a secondary sexual characteristic that prohibits mating. The experimental removal of the wings from gynes of another fungus-growing ant species, *Acromyrmex echinatior*, prompted a behavioral repertoire shift where wing-clipped gynes carried out worker tasks (Nehring & al. 2012). If castrated, gynes complete tasks for the betterment of the colony, as the worker caste does. These individuals then serve the social parasite's interests by remaining in the nest and not dispersing. This type of behavioral alteration is most likely seen in parasites that are dependent on their host for long periods of time (Baudoin 1975) as is the case in *M. adamsae* and *Megalomymex symmetochus* Wheeler, W.M., 1925. The same would be true for endoparasites that require a long developmental time period inside the host. Although wing clipping has been observed in two *Megalomyrmex* guest ant social parasites (Adams & al. 2012, Adams & al. 2013, Boudinot & al. 2013) it may also be found in other guest ant social parasites (e.g., *Formicoxenus*, *Polyrhachis*) or in inquiline parasites that live beside rather than kill their host queen. Searching for castration by social ant parasites in other systems, especially when the parasite remains in the host nest for many years may prove fruitful.

Discussion

Parasite-induced changes of host behavior in ecologically significant social insect species provide broad-scale insights for the potential impacts of host-parasite interactions. The nematode *Sphaerularia bombi* Dufour, 1837 castrates bumblebee queens. Before they are killed, the queens are controlled by the parasite that dysregulates instinctual digging behavior in the bee to favor nematode reproduction rather than their own (Poinar & Van der Laan 1972, Lundberg & Svensson 1975). Such modifications of host behavior have ecological repercussions as pollinator species have wide-ranging impacts (Kadoya & al. 2015). Equally, or perhaps more, significant are ant species with huge colonies that can make up over half the animal biomass (Hölldobler & Wilson 2009) and heavily influence nutrient flow in tropical rainforests (Griffiths & al. 2018). Like honeybees and bumblebees, a range of parasites target ants. However, most ant parasites are yet to be discovered as the frequent motivation to study them stems from biocontrol efforts against specific invasive species and pests. Moreover, the behavioral effects of parasite pressures and infections at the individual-ant and colony level and the repercussions for colony fitness and possibly the ecosystem processes that ants are involved in, are vastly underexplored. Parasites affect colony fitness, albeit indirectly, when their interactions with individuals lead to a reduction of participation in caste-level tasks that benefit the colony. Moreover, the colony's defenses against competing conspecifics, social parasites and parasitoids can be lowered because of parasite-induced changes. Such parasite pressures could be missed when research

questions only focus on colony-level behavior and experiments are done with multiple ants from the same colony to average out idiosyncratic behaviors. Recognizing and acknowledging abnormal behaviors of individual ants, by further investigating them, could thus lead to the discovery of novel parasites, as well as a better understanding of caste-level behaviors and their impact on colony fitness.

Though reports of evident parasitic modification of ant hosts do exist (Tab. 1), they are missing critical data that allow an understanding of individual- and colony-level fitness impacts. In fact, in some cases, host modifications are so severe that myrmecologists initially misinterpreted the taxonomy of parasitized individuals. For example, *Cephalotes atratus* ants having berry-like gasters filled with *Myrmeconema neotropicum* were originally misdiagnosed as a novel variety (Poinar & Yanoviak 2008), and nematode-infected *Pheidole pallidula* with enlarged gasters and reduced aggression were first thought to be social parasites (Borowiec & Salata 2015). Perhaps, a closer inspection of abnormal individuals in other ant species may reveal new parasites as well. Alternatively, broad screening with molecular tools would help elucidate the prevalence and abundance of parasites, and provide a more accurate estimate of the selection pressures involved in an ant colony, at least due to parasites. This could then be followed by colony-level observations, comparing how infected and uninfected individuals behave.

The abnormal behaviors resulting from an infection can be adaptive to the parasite, adaptive to the host, or a mere side-effect with no clear function. Rigorous experimental testing and observation are thus required to decipher where host response ends, and parasitic manipulation begins. Even in what may seem to be textbook examples of host manipulation, a deep understanding of the mechanisms and fitness outcomes are not always well understood. Nematomorph-manipulated water-seeking crickets have been leveraged to probe the important distinction between parasitic manipulation and host response. Biron & al. (2005b) compared reproductive capability for hosts that were allowed to release the parasite in water and hosts that did not have access to water. They concluded there were no meaningful fitness benefits to "collaboration" with the parasite, and the hosts are indeed manipulated by the nematomorphs. These conclusions even err on the conservative side. Factors such as the risks of predation of infected hosts (Sato & al. 2011a) and possible host castration have clear consequences for host and parasite but are often ignored. Carefully designed experiments to assess fitness outcomes are desirable and necessary to consider the adaptive significance of proposed host manipulations by parasites.

Integrative efforts that combined behavioral assays with next-generation sequencing have resulted in candidate genes and pathways that are possibly involved in the altered behavioral outcomes upon infection, offering exciting new insights. In addition, the Global Ant Genomics Alliance will sequence ca. 200 ant species, in addition to the 20 already completed, by 2020 (Boomsma & al. 2017). Efforts for sequencing 100 - 200 more species are being encouraged, thus, potentially hundreds of high-quality genome assemblies are on the horizon. With these genomic resources, future studies can better integrate "-omics" data with behavioral ecology, advancing our understanding of the molecular mechanisms that parasites use to adaptively influence their hosts, and additionally reveal how ant behavior is controlled and regulated. Moreover, such endeavors could demonstrate that similar molecular strategies have evolved across parasite-ant interactions that show behavioral parallels. The next step, to ascertain function and involvement of found candidate genes and compounds, would be to design gene function assays. Such efforts will be easier in some, and more difficult or likely impossible in other systems. However, because of the many parallels that can be found among the behavioral outcomes of a wide variety of infections, detailed investigations into more experimentally approachable systems could potentially be informative to other, less approachable ones, as well.

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