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**THE ECOLOGY, EPIDEMIOLOGY, AND EVOLUTION OF PARASITES INFECTING
ANTS (HYMENOPTERA: FORMICIDAE)**

A Dissertation in
Biology
by
Lauren E. Quevillon

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The dissertation of Lauren E. Quevillon was reviewed and approved* by the following:

David P. Hughes
Associate Professor of Entomology and Biology
Dissertation Advisor

Andrew F. Read
Evan Pugh Professor of Biology and Entomology,
Eberly Professor of Biotechnology
Chair of Committee

Jessica M. Conway
Assistant Professor of Mathematics
Outside Field/Unit Committee Member

Peter J. Hudson
Willaman Professor of Biology,
Director of the Huck Institutes of Life Sciences
Committee Member

Stephen W. Schaeffer
Professor of Biology
Associate Department Head of Graduate Education

*Signatures are on file in the Graduate School.

Abstract

Ants (Hymenoptera: Formicidae) are one of the most ecologically dominant groups of organisms on Earth, despite being characterized by life histories that exacerbate the potential for infectious disease epidemics. Understanding how ants have interacted with their parasites over ecological and evolutionary time is crucial for understanding their ecological success. My dissertation aims to advance our knowledge by investigating three broad questions: (1) which parasitic organisms infect ants and what are their associated life history and ecological traits, (2) what are the epidemiological impacts of these parasites on colony functioning, and (3) how do ants mitigate the impacts of their interactions with parasitic organisms.

First, I extensively survey the known pathogens, parasites, and parasitoids of ants (hereafter ‘parasites’) and find that most parasites require the death of individual ant hosts as a developmental necessity, only need one ant host to complete their life cycle, and must leave the nest before transmitting to their next ant host. I find that most parasites infecting ants come from the Order Diptera, Phylum Fungi, and Order Hymenoptera, and there are very few viruses and bacteria known to infect ants. I also find that our knowledge of parasites infecting ants is very poor- out of 333 recognized ant genera, only 81 have parasites reported to infect them.

Next, I model the epidemiological consequences of the most prevalent parasite transmission mode, parasites transmitting outside the nest, on ant colony dynamics. Using a deterministic modeling framework, I explore how colony birth rate, parasite infection rate, the proportion of the colony foraging, and parasite seasonality impact colony growth dynamics. I find that for biologically reasonable parameter values, colony collapse is not predicted to occur, suggesting that the majority of parasites known to infect ants may not be posing a significant threat to colony survival, though their impacts on colony-level phenotype and fitness remain unknown.

I extend this work to model the consequences of the few parasites of ants known to use direct, nest-mate to nest-mate (*‘in-nido’*) transmission strategies by using a stochastic modeling approach. I find that contrary to the *‘ex-nido’* parasites modeled previously, colony collapse is much more likely to occur. However, I find that collapse can be mitigated through the use of two behavioral defenses that ant colonies have in

their arsenal: social avoidance and cadaver management.

Finally, I investigate whether ant colony organization might be optimized to reduce the transmission of infectious diseases by using social network analysis to understand carpenter ant social and spatial organization in the absence of disease. I focus on trophallaxis, the oral sharing of food, as the key social interaction of interest because ant colonies must balance efficient food flow with reducing disease transmission. First, I assess whether forager ants, which serve as potential carriers of infectious agents, behave differently in their network interactions and nest spatial usage than their non-foraging nest mates. I find that foragers are both socially and spatially distinct from their non-foraging counterparts, and never engage in direct interactions with queens. Next, I extend this work by investigating whether the temporal structure of ant trophallaxis networks might be protective through either temporal or social filtering processes. I find that while foragers and queens are socially segregated, there is no evidence for nuanced organizational immunity through the temporal structuring of ant trophallaxis networks.

This dissertation synthesizes our current knowledge of parasites infecting ants and provides theoretical models for how these parasites epidemiologically interact with their hosts, providing the foundation for future empirical studies.

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Dedication

This dissertation is dedicated to all of the natural historians who build our foundational knowledge of biology. While working on this dissertation, I compiled hundreds of records of parasites infecting ants, which were collected by passionate scientists over several centuries. Without these natural historians, the work of this dissertation would be impossible. As I read through their manuscripts, I felt like I developed a personal relationship with these individuals, some of whom passed many years ago. It felt oddly touching to cite them, and to know that their work, though often underappreciated, has achieved a special kind of immortality.

CHAPTER 1

1

Introduction

Infectious disease outbreaks are a common constraint of group living organisms. The increased frequency of potentially infectious contacts coupled with the buildup of infectious fomite favor a positive correlation between group size and disease [1–3]. However, infectious disease outbreaks may not necessarily be an unavoidable consequence of evolving to live in dense groups. The ants (Hymenoptera: Formicidae) are one of the oldest lineages of social animals on Earth, having transitioned from solitary living to eusociality 115 - 168 Ma [4]. Throughout their evolutionary history, ants have had to contend with pressure from pathogens, parasites, and parasitoids, many of which were diversifying and co-evolving alongside their hosts. Despite this pressure, the ants are one of the most successful groups of organisms [5, 6] and disease outbreaks in ant colonies are rarely observed. Thus, the ants and their parasites offer an important case study for investigating the ecological and evolutionary relationships of pathogens and parasites with their social hosts.

In this chapter, I introduce the ants as one of the most dominant social groups on Earth. I highlight the ways in which they are ecologically important and detail some of the mechanisms that underlie their longstanding success. Next, I discuss the general, positive relationship between sociality and disease in all social organisms, and highlight reasons why ant colonies might be particularly vulnerable to epidemic outbreaks. I then summarize the many defense mechanisms, both individual and social, that ants use to contend with the parasite pressure that they face. Finally, I outline the aims of my dissertation and show how they advance our knowledge of how ants and their parasites have interacted over evolutionary time. It is my hope that this

work has broad relevance to our understanding of sociality and disease generally, with the ants representing a comparative foil to other, better studied, social animal groups.

1.1 Ecological success of the ants

The ants are one of the most successful lineages of organisms on Earth [5, 6]. They are an incredibly diverse family, with over 13,000 described species in 333 recognized extant genera [7], with many additional species awaiting description [5, 7]. Ants make up a significant proportion of the insect biomass [8, 9], particularly in tropical rainforests [10, 11]. They also have a wide geographic range; only a handful of places, such as Hawaii, lack native ant species [5, 12] and they are dominant in both disturbed and pristine environments [5, 13, 14].

As such, ants are major players in the communities and ecosystems in which they live. Ants are found in every terrestrial habitat, from deep subterranean nests in dry savannah grasslands to tropical forest canopies [5]. Ants are the leading predators of terrestrial invertebrates [5, 15, 16]. They are also fungivores, having developed one of the first forms of agriculture over 50 million years ago [17, 18], and herbivores, tightly linked to their bacterial mutualists [19]. Ants participate in elaborate and diverse symbioses: tending hemipterans for their honeydew exudate in exchange for providing protection [20], removing pathogens from the fungi that they farm [21], housing the many myrmecophiles that live within their nests [22], and defending plants against herbivory [23].

Through their ecological interactions, ants exert both bottom-up and top-down control in communities and can act as ecosystem engineers [13]. For example, by transporting leaves and debris into their large underground nests, leafcutter ants in the genus *Atta* circulate far more nutrients and minerals through the soil than would otherwise occur, resulting in a four-fold increase in the number of tree roots grown than in undisturbed soil [24]. Ants can also shape the distribution of plants through their role as seed dispersers [25] and can negatively impact bird abundances by outcompeting them for food resources [26, 27]. Together, this body of evidence demonstrates that ants are a successful and ecologically impactful animal group.

1.2 The rise of the ants and origins of eusociality

The ecological success of the ants is a product of the innovations they accrued over their long evolutionary history. Ants evolved from an aculeate (stinging) wasp ancestor [28, 29] and extant Formicidae first arose between 140 - 168 Ma, in the Late Jurassic or Early Cretaceous periods [4]. Major ant subfamilies did not begin to diversify until the Late Cretaceous or Early Eocene, concordant with the rise of the angiosperms [4, 30].

Eusociality, the highest level of social organization and a significant evolutionary achievement [31], has arisen multiple times across the animal phylogeny [32–37]. Eusociality is defined by the presence of a division of labor, cooperative brood care, and overlapping generations [5, 38, 39]. In the case of the ants, eusociality arose at the origin of the Formicidae [5, 35, 40–42] and all extant ants are eusocial [5]. For the ants, the evolution of eusociality likely occurred via the subsocial route [43], involving a sequence of increasingly social lifestyles in which females went from simply laying eggs near paralyzed prey, to constructing nests and progressively provisioning larvae with prey items, to overlapping generations with eventual behavioral and physical division of labor [5, 40]. Inclusive fitness and high genetic relatedness were critical to the evolution of eusociality, because the indirect fitness benefits individuals received by caring for related individuals likely exceeded those gained from living solitary lifestyles [44–47]. Once eusociality evolved in the Formicidae, it opened up many opportunities for subsequent evolutionary innovation.

1.3 Ant colonies benefit from an effective division of labor

The evolution of eusociality, in which there is a marked division of labor, has been pivotal to the ecological success of the ants [48]. This division of labor preceded the evolution of a reproductive division of labor, with reproductive castes focused on reproducing colony members and sterile worker castes that specialize in particular tasks. Together, this division of labor and reproduction makes colonies more efficient at converting energy into new colonies [5, 49]. Ant colonies regulate their division of labor in a variety of ways, both temporally and behaviorally, as well as physically. Most ant species employ some degree of age-related polyethism, in which workers

transition through tasks as they age, though this is much less pronounced in ant colonies compared to bee colonies [50]. For example, younger workers tend to perform comparatively safe intranidal tasks such as brood care and nest maintenance, only transitioning to the relatively risky task of foraging once they have aged [5, 51]. Task specialization can be behaviorally reinforced through variations in response thresholds [52] and inter-individual differences in personality [53, 54], as well as through learning [55–57]. Finally, in about 15% of ant genera, division of labor is further accomplished through caste polyethism, in which certain tasks are performed by different physical castes [5, 38, 58]. For example, many species of army ants have a soldier caste with larger heads and mandibles dedicated to colony defense and moving large prey items [5] and ants in several genera have specialized ‘honey pot’ workers with expandable abdomens that serve as living food silos [5].

Importantly, though ant colony division of labor is organized temporally, behaviorally, and physically, it has built-in redundancy and remains flexible despite individual specialization. Ant colonies generally accomplish tasks in a ‘series-parallel’ manner, in which each step in a given task is completed by multiple workers so that the loss of any one individual does not hinder task completion [5, 58]. Individuals specialized on one task still retain enough behavioral flexibility to accomplish other tasks as needed. For example, Wilson [59] modulated the caste ratio in leafcutter ant colonies and found no loss in foraging efficiency. Ugelvig and Cremer [60] found that fungal-infected workers ceased brood care, and uninfected nest mates assumed the role in their place. The redundancy and flexibility inherent to ant colony division of labor are likely key to their resilience in the face of perturbation, but we still lack an understanding of exactly how colonies buffer the loss of individuals and what the upper limits of this buffering capability are.

Though eusociality engenders an efficient division of labor, one complication is that the work normally accomplished by one organism is instead being accomplished by a ‘superorganism’ [61]. This superorganism, comprised of hundreds to millions of individuals, lacks top-down control; no single individual regulates the internal functioning of ant colonies [62]. Rather, ant colonies are complex systems [62–68] in which individuals operating by simple rules interact to create sophisticated emergent behavior at the level of the colony. Though the behavioral repertoire of each individual ant is relatively small [5], ant colonies are able to create elaborate nests [69], forage efficiently [70], cooperatively move prey much larger than themselves [71], and

become living architectural structures in response to environmental challenges [72]. Thus, the lack of centralized, top-down control is actually a positive, allowing for colony-level behavior that is far more sophisticated and dynamical than could be otherwise achieved by a single insect.

1.4 Increased disease burden is considered to be a major cost of sociality

Though the transition from solitary living to eusociality at the origin of the Formicidae enabled the innovation of many beneficial traits, the adoption of a social lifestyle is not without costs. The largest assumed cost of group living among many animals is the increased burden of infectious disease, due to the higher density and frequency of potentially infectious contacts [3, 73–80]. Furthermore, as social groups defend home territories and colonies, build-up of infectious fomite can intensify parasite pressure [3, 81]. ‘Parasite escape’ from pathogen buildup in home nesting sites might be one reason for the occurrence of animal migrations [82–84]. Thus, as group size increases, there is a generally positive increase in parasitism [2, 3, 85, 86]. However, it is being increasingly recognized that the relationship between sociality and disease is not always linear and that additional factors, such as group structure, are important for modulating their relationship [79, 80, 87].

Ant colonies have several features that might make them more vulnerable than other social groups to infectious disease outbreaks. Colonies range in size from hundreds to millions of individuals [5, 88, 89], and due to their haplodiploid genetic structure, have a higher average genetic relatedness to one another than other animal groups [5]. The ancestral nesting ecology of ants was in soil, necessitating prolonged contact with potentially pathogenic microbes [90]. Additionally, the majority of ants are central place foragers with limited nest relocation [5], allowing for the buildup of infectious fomite.

Ants are known hosts to a wide array of pathogens, parasites, and parasitoids [22, 91]. However, our understanding of how these parasites interact with their ant hosts at either the individual- or colony-level remains poor. For example, we do not know whether most of these parasites are capable of transmission inside ant colonies, or whether death of the ant host occurs in most infections. We do not know which

groups of organisms predominantly parasitize ants, or which genera of ants are the most parasitized, nor do we know how ants and their parasites have co-evolved over time. We don't know how ant parasite species richness scales with latitude, or what host traits might be correlated with parasitism by certain parasite taxa. Though our knowledge of ants and their parasites remains scarce, the great ecological success of the ants over evolutionary time implies that despite the multiple factors that could promote disease, ants in some way effectively manage their disease burden.

1.5 Ants have effective individual and social immune defenses

Having effective disease defense mechanisms was likely a prerequisite for the Formicidae to transition from solitary living to eusociality [92]. Though there is a correlation between group size and parasite intensity and prevalence [1–3] living in a social group can reduce per-capita investment in prophylactic immune defenses [93], or mitigate the impact of infection [94, 95]. In addition, parasite pressure probably facilitated the evolution of novel social behaviors that function to reduce parasite exposure or infection, a form of 'social immunity' (reviewed in [91, 96–99]). Below I review the individual and social immune mechanisms that ants have in their defense arsenal.

Individual immune mechanisms

Insects have a suite of physiological immune mechanisms at their disposal [100]. Insects are capable of recognizing self from non-self through the recognition of pathogen-associated molecular patterns (PAMPs) (reviewed in [100]). Following recognition, insect immune systems respond through a variety of mechanisms, including but not limited to phagocytosis, melanization, and encapsulation, as well as through the release of antimicrobial peptides, reactive oxygen species, and lytic enzymes, which are themselves the products of molecular and cellular pathways (i.e. Spatzle-Toll, Imd, JAK/STAT) (reviewed in [100]).

Though innate immunity is traditionally thought of as non-specific, innate immune responses in several insect species have been shown to be both specific and long-lasting [101, 102] (reviewed in [103]). Furthermore, some insects have demonstrated immune priming, in which the introduction of a dead or live-attenuated mi-

crobe leads to the up-regulation or ‘priming’ of microbial pattern recognition proteins and the production of antimicrobial peptides [101, 104–106], conferring a protective effect when individuals are subsequently immune challenged (reviewed in [103]). The generality and longevity of these protective effects is unknown and might not apply to all host-pathogen systems (e.g. no evidence of immune priming in fungus-infected ants, [107]). A further extension of this is trans-generational immune priming, in which parental exposure to microbes confers protective benefits to their unexposed offspring and has been demonstrated for several insect species [108–114] (reviewed in [115, 116]).

In addition to traditional immunological defenses, ants also produce and consume chemicals that aid in anti-pathogen defense (reviewed in [117]). The metapleural gland is an exocrine gland unique to ants (though it has been secondarily lost by some ant genera) that secretes many different acids, alcohols, and ketones (reviewed in [118, 119]). Many of these secretions have measured antimicrobial activities [120]. Fernandez-Marin et al. [121] surveyed 26 different species of ants and found that all actively applied metapleural gland secretions to their body, and some applied these secretions onto nestmates and brood as well. Indeed, when ants had their metapleural gland blocked, their survivorship following a fungal challenge decreased significantly [122]. Ants also have an acidopore that produces venom; and similar to the secretions of the metapleural gland, these venoms have antimicrobial properties [123, 124] which benefitted ant survival when faced with pathogen challenges [125]. Coupled with their own individual immune and chemical defenses, ants have been shown to ‘medicate’ themselves by consuming substances that increase survival when infected by pathogens but which are harmful in the absence of infection [126]. Thus, even individual ants have an impressive suite of prophylactic and inducible anti-parasite defenses.

Social immune mechanisms

Despite the positive correlation between group size and parasite prevalence, living within a group can confer benefits to both uninfected and infected individuals. A quest to uncover mechanisms by which ants and other social insects might collectively mitigate disease outbreaks has driven research over the past thirty years. Together, this body of work has revealed an impressive array of defenses, termed ‘social immunity’,

that serve to reduce the introduction and onward transmission of infectious agents within colonies (reviewed in [91,97,99,127–129]). These defenses include physiological, behavioral, and organizational mechanisms, reviewed below.

One hallmark of ant colonies is that not all members leave the protected confines of the nest. Some individuals (e.g. foragers) can become exposed to pathogens in sub-lethal doses in the extranidal environment and mount individual immune responses as detailed previously. Ants are able to share some of these individually-mounted immune resources with each other through social immunization. For example, it has been shown that ants exposed to a non-lethal immune challenge increased the amount of social food sharing, or trophallaxis, that they participated in [130, 131], and these trophallactic droplets had increased antimicrobial activity, which conferred higher survivorship to their unexposed nest mates [132]. It has also been demonstrated that ants can transmit sub-lethal doses of pathogen to their unexposed nest mates, eliciting an immune priming response that was protective upon subsequent infection [133, 134]. However, some counterexamples exist, drawing into question the generality of such social immunization across host-parasite systems. For example, Mirabito and Rosengaus [135] found that when termites engaged in proctodeal trophallaxis, the anus-to-mouth sharing of fluids, with nestmates that had been immune challenged, they were significantly more likely to be susceptible to subsequent immune challenges.

In addition to sharing immune modulators, ant and other social insect colonies have a suite of behavioral defenses in their social immune arsenal. Self- and allogrooming are effective ways to remove infectious particles in order to prevent infection [60, 125, 136–140]. If infection does occur, the onward transmission of disease can be prevented by social isolation of healthy and infected nest mates [141–143]. For example, Ugelvig and Cremer [141] showed that fungus-infected ants ceased brood care and avoided the brood chamber, while Rueppel et al. [142] showed that diseased honey bee workers altruistically removed themselves from their colonies.

Sometimes prophylactic and behavioral avoidance measures are not sufficient and colonies can choose to either chemically disinfect or kill infected nestmates [144–146]. For ants that die of infection or natural causes within the colony, effective corpse management is essential (reviewed in [147]). Ants remove corpses from their colonies [5, 148–151] and disinfect corpses through chemical (e.g. spraying formic acid) and mechanical (e.g. destroying or burying) means.

Finally, it has been posited that the social and spatial organization of social insect

colonies is itself designed to prophylactically reduce the spread of disease [91, 97, 129]. While the concept of ‘organizational immunity’ is enticing, the extent to which it is employed by colonies remains unknown. Social insect colonies are spatially segregated, with foragers spending their time near the nest entrances while the queen(s) and brood are located in the interior of the nest [152, 153]. Theoretical work has shown that indeed, spatial organization of ant colonies could serve to reduce intra-colony pathogen transmission [154–157]. While spatial segregation appears to play a prophylactic role in preventing disease transmission, little is known about whether social segregation also occurs. The sharing of liquid food (trophallaxis) is a particularly important behavior of interest because colonies must balance the efficient distribution of beneficial resources throughout the colony with mitigating potential parasite transmission. Trophallaxis networks have not yet been assessed for the potential presence of organizational immunity.

1.6 Dissertation objectives

My dissertation aims to contribute to our knowledge of how social hosts interact with their parasites over ecological and evolutionary time using the ants and their diverse array of parasites as a case study. In this work, I investigate three broad questions: (1) which parasitic organisms infect ants and what are their associated life history and ecological traits, (2) what is the epidemiological impact of these parasites on colony survival, and (3) how do ants mitigate the impacts of their interactions with parasitic organisms. The field of infectious disease ecology and evolution has often focused on social organisms within the class Mammalia; our understanding of general ecological and evolutionary principles will benefit from including one of the most dominant social groups on Earth.

In Chapter 2, I comprehensively survey the known pathogens, parasites, and parasitoids of ants (hereafter ‘parasites’). Ants are known to be hosts to a diverse array of parasites, but the relative taxonomic diversity of these parasites is unknown, as is how they assort throughout the phylogeny of the ants. Importantly, I include relevant parasite life history details alongside host records, such as mode of infection, parasite transmission strategy, and impacts on host morbidity and mortality so that general epidemiological trends of parasites infecting ants can be uncovered.

In Chapter 3, I model the epidemiological consequences of the most prevalent

parasite transmission mode on ant colony dynamics. I create a deterministic mathematical model of an age-structured ant colony and then model the consequences of parasites that use '*ex-nido*' transmission, in which nest mates are incapable of directly infecting one another inside the colony and only foraging ants are potentially exposed. I explore how colony birth rate, parasite infection rate, the proportion of the colony foraging, and parasite seasonality impact colony growth dynamics. Chapter 4 extends the work of Chapters 2 and 3 by modeling the consequences of the few parasites of ants known to use direct, nest-mate to nest-mate or '*in-nido*' transmission strategies. Using a stochastic compartmental model of an age-structured ant colony, I assess the likelihood of colony collapse in the presence of two behavioral defenses that could mitigate disease transmission: social avoidance and cadaver management.

In Chapters 5 and 6, I investigate whether ant colonies exhibit evidence of prophylactic organizational immunity by using social network analysis to understand carpenter ant social and spatial organization in the absence of disease. Chapter 5 makes use of trophallaxis (food sharing) networks to see whether forager ants, which serve as potential carriers of infectious agents, behave differently in their network interactions and spatial usage within nests than their non-foraging nest mates. In Chapter 6, I extend this work by investigating whether there is evidence of organizational immunity in the temporal structure of ant trophallaxis networks and in the resulting functional flow of resources through the observed network structure. In chapter 7, I synthesize the work of my dissertation and provide a discussion of future research directions.

**Pathogens, parasites, and parasitoids of ants-
a review and synthesis of parasite biology and host
records**

2.1 Abstract

Ants are among the most ecologically successful organisms on Earth, due to their eusocial life style, effective division of labor, and emergent, colony-level behaviors. Despite the benefits of group living, the increased burden of infectious disease is presumed to be a major cost, with parasite prevalence and intensity scaling positively with group size. To understand the ecological success of the ants, we need to understand how they have mitigated the costs of infection by parasitic organisms over their evolutionary history. As a first step, we need to know what parasitic organisms infect ants, and how they interact with their hosts. Here we provide a comprehensive review of the parasitic organisms infecting ants by collecting all extant records and we synthesize major patterns in parasite ecology by categorizing how parasites encounter their ant hosts, whether they require host death as a developmental necessity, and how they transmit to future hosts.

We report 1,415 records of parasitic organisms infecting ants, the majority of which come from Order Diptera (34.8%), Phylum Fungi (25.6%), and Order Hymenoptera (25.0%). Most parasitic organisms infecting ants are parasitoids (89.5%), requiring the death of their host as developmental necessity and most encounter their hosts in the extranidal environment (68.6%). Most parasitic organisms infecting ants only need

a single host to complete their life cycle (89.1%), but importantly, we found that the vast majority need to leave the nest before transmission to their next ant host (88.3%), precluding ant-to-ant transmission within the nest. With respect to the host, we only report records for ants in 10 out of the 17 extant ant sub-families, and for 81 out of the currently recognized 333 ant genera. Though there is likely bias in the records reported, both host and parasite ecological traits and evolutionary histories underlie the pattern of ant-parasite association reported here. This work provides a foundation for future work that will begin to untangle the ecological drivers of ant-parasite relationships and the evolutionary implications thereof.

2.2 Introduction

Ants (Hymenoptera: Formicidae) are among the most ecologically successful organisms on Earth [5, 6, 158]. They account for a significant proportion of total insect biomass [8–10], and are important constituents of ecological communities [5, 13, 15]. Ants inhabit almost every terrestrial ecosystem [5, 12], have diverse nesting and foraging ecologies [5], and are speciose, with over 13,000 extant species in 333 genera [7].

Modern ants (Hymenoptera: Formicidae) first arose 140 - 168 Ma [4, 30] from solitary wasp ancestors [28, 29]. At their origin, ants evolved eusociality [5, 35, 40–42], which is defined by a division of labor, cooperative brood care, and overlapping generations [38]. The transition to eusociality marks a significant evolutionary achievement [31]; only a handful of lineages have attained that level of social organization [32–37]. Eusociality has been crucial to the ecological success of the ants by allowing for an efficient division of labor [5, 49, 58] and for emergent, complex behaviors at the level of the colony [62–68].

However, social living is not without costs, the largest of which is thought to be the increased burden of infectious disease, due to the increased frequency and density of potentially infectious contacts [3, 73–80]. Extant ant genera are known hosts to a variety of parasitic organisms [22, 91], and their solitary wasp ancestors were also likely host to parasites as well. As the ancestral ants transitioned to their increasingly social lifestyle it is reasonable to assume that this offered enhanced opportunities for disease transmission but also fostered the innovation of anti-parasite defenses, many of which were likely in place prior to the transition to eusociality [92]. When the angiosperms arose in the Late Cretaceous, ants rapidly diversified to occupy newly

available ecological niches [4]. This diversification pushed ants into novel habitats and into contact with novel parasites.

The ecological success of the ants has likely depended on their ability to effectively mitigate the costs of infection by parasitic organisms. Selection pressure from these parasites facilitated the evolution of new defenses, both physiological and behavioral, at the individual and colony level (reviewed in [91,97,99,127–129]). Thus, to understand the ecological success of the ants, we need to understand their relationship with their parasites, both ecologically and over evolutionary time.

Parasites have been increasingly recognized as important members of communities and ecosystems [159–161]. Understanding drivers of parasite richness and community composition, as well as their cascading impacts, depends on understanding the ecological relationships they have with their hosts [162]. Furthermore, parasites are very important shapers of the evolutionary ecology of their hosts [163, 164]. While parasites of many other social organisms (e.g. humans, lions, wolves) have been extensively studied, ants have been underappreciated in their role as host to a wide range of parasites. The diversity of ant ecologies [5], coupled with their well-resolved phylogeny, makes the ants fertile ground for studying general principles of parasite evolutionary ecology.

2.2.1 Defining relationships: pathogens, parasites, parasitoids, and predators

In order to understand the ecology and evolution of ants and the organisms that associate with them, we first must explicitly define our terms of association. There are many ecological relationships in which one interacting partner benefits at the expense of another, and the terms for these, such as ‘pathogen’, ‘parasite’ and ‘parasitoid’ have often had shifting definitions (see discussion within [163, 165, 166]). There has historically been a distinction between ‘micro-parasites’ (or pathogens), which have short generation times, directly reproduce within the host, and generate stronger immune responses, and ‘macro-parasites’, which have longer generation times, typically do not reproduce directly within the host, and do not generate long-lasting immune responses [167]. The term parasitoid is applied where host death is a developmental necessity [168]. Additional terms have been added in to describe, for example, the location of the parasite in relation to the host (endo-, ecto-, meso-)

or whether the host keeps developing following parasitization or if development is arrested (koinobiont vs idiobiont, respectively). Many of these definitions have been implicitly taxon-restricted (i.e. viruses, bacteria and fungi are discussed as pathogens, whereas helminths are parasites and insects are discussed as parasitoids).

Recently, work has attempted to understand generalities in trophic strategies [166, 169] by unifying predators, parasites, and parasitoids through general consumer-resource theory. This has provided clarity in how distinctions between these terms are made. We follow this work and base our definitions of host relationship (Table 2.1) on whether consumers feed on one or more hosts during a give life stage (predator vs. parasitic organism), and whether the loss in host fitness is partial or complete (parasite vs. parasitoid). While all of those terms involve some loss of host fitness, this issue becomes complicated for ants and other social insects as fitness lies at the level of the colony and not at the level of the individual [170]. Though it remains unclear how the impact of a sick or dead ant cascades up to effect lifetime colony-level fitness, for the purposes of simplicity and to facilitate comparison to other host systems, we consider individual ants as hosts.

For this work, we consider three major categories of association between ants and other organisms (Table 2.1), based on the number of individual hosts they interact with during a given life stage and the degree that they impact host fitness. Parasites interact with one host in a given life stage, and cause some loss to host fitness. Parasites can occasionally cause host death, but it is not a developmental necessity. In this work, we do not make a distinction between pathogens and parasites, as they are functionally equivalent when considering the two criteria listed previously. Strepsipteran insects are an example of a parasite infecting ants. Males develop inside ants and emerge from the host following eclosion. The emergence of the strepsipteran does not require host death, but the host often dies indirectly due to secondary infection by opportunistic fungi. In contrast, parasitoids also interact with one host in a given life stage, but they cause host death a developmental necessity. Though the term parasitoid has been historically applied only to insects, this is not logical [166]. For example, the zombie-ant fungus *Ophiocordyceps* can be considered a parasitoid, as it requires the death of the ant before it can create its reproductive structures [171]. The differences between parasites and parasitoids can often be nuanced; for example, Beani et al. [172] showed that a strepsipteran was functionally a parasite when it infected male paper wasps, but when it infected female paper wasps, its development caused the reproductive

castration of its host and thus functioned as a parasitoid. Finally, though they are not a targeted focus of this current work, if we found records of predators inside ant nests, we included them for interested readers. Predators consume multiple hosts in a given life stage, causing complete loss of host fitness via host death. In the case of whole ant colonies, predators could be considered parasites of the superorganism, but here we only consider the host at the level of the individual ant. Thus, microdon larvae (Hymenoptera: Syrphidae), which live inside ant nests and consume multiple eggs and brood, would be considered predators.

It is also important to note that the association of one organism with another is often life stage dependent. For organisms that use multiple hosts in their life cycles, the relationship with one host can be drastically different from their relationship with another. For example, many tapeworms (Cestoda) cause little pathology to their vertebrate final hosts and thus are generally considered to be parasites, but because they require their invertebrate intermediate host to be consumed for transmission to occur (trophic transmission), they would be classified as parasitoids when infecting ants. In this work, we categorize associations based on the relationship of organisms with their ant host, according to the criteria in Table 1.

2.2.2 Additional relationships: myrmecophiles, social parasites,inquilines, and nest associates

Ants have other relationships with diverse commensals, mutualists, and parasites that live inside their nest and associate with the entire colony rather than just a single individual (Appendix A.2). The term myrmecophile can refer to any of the numerous organisms that are dependent on ants for any portion of their life cycle [173], though the term is usually restricted to animals that live inside ant nests. These include social parasites, defined here broadly as any insects that live inside ant nests and exploit colony resources to the detriment of their ant hosts [5, 174], as well as inquilines, who are workerless ant species whose queens live inside the colonies of other ants species (reviewed in [175]), and nest associates, vertebrates and invertebrates who live inside ant nests and whose relationships with ants are largely unknown. Thomas et al. [174] estimate that 10,000 - 20,000 morphospecies of insects have evolved to be social parasites of ants. To review those associations is beyond the scope of this work. Interested readers are directed to the reviews within Holldobler and Wilson [5],

Schmid-Hempel [91], and Thomas et al. [174]. Occasionally, when searching for parasites and parasitoids of ants, associations would be reported that were unclear. We report these simply as ‘associates’, and identify them as areas where additional biological details are needed.

2.2.3 Gaining access to ant hosts

Ant colonies are generally thought of as ‘factory-fortresses’, [176] well-protected against threats from both other species and con-specifics alike [5]. For some parasitic organisms, encountering hosts can occur readily as ants forage outside their nest; for others, the process is more difficult, requiring sophisticated chemical mimicry to break into the colony ‘fortress’. The subject of how parasites and parasitoids gain access to hosts has been well reviewed within Schmid-Hempel [91]. Here our goal is to simplify categorization so that large-scale patterns can be found, and to that end we define three overarching categories of how parasitic organisms and their ant hosts encounter one another (Fig. 2.1). In defining these encounter types, it is important to distinguish where the initial contact of host and parasitic organism happens relative to the nest (i.e. does the encounter happen inside the nest or outside of it). This is particularly important for ants and other social insects, because many colony members (i.e. brood, younger nest workers) do not leave the protected confines of the nest, thus limiting potential encounters with parasites.

In primary encounters, the parasitic organism directly encounters an ant host in the extranidal environment and infects that ant. Two examples of this are when a foraging ant walks over fungal spores (e.g. *Ophiocordyceps*) and subsequently becomes infected, or when a phorid fly oviposits (e.g. *Pseudacteon*) directly into an ant (Fig. 2.1). In secondary encounters, the parasitic organism encounters an ant host in the extranidal environment, becomes attached to that ant (either internally or externally), and is then transported (phoresy) back inside the colony where it infects a different individual (Fig. 2.1). Examples of this include some cestode species (e.g. *Raillietina*), where adult ants pick up proglottids in the environment and then bring them back to feed to brood, or the larvae of some eucharitid wasps (e.g. *Pseudochalcura*), which are transported back into the nest where they develop on or inside brood. Finally, encounters are scored as independent when the parasitic organism enters the intranidal environment independently and subsequently infects ant hosts. An example

of parasitic organisms using independent encounters are adult mutillid wasps (e.g. *Ponerotilla*) which enter ant nests on their own and oviposit inside them, or eucharitid wasps in the sub-family Oraseminae (e.g. *Orasema*), which phoretically attach to thrips or other hemipterans that then gain access to ant nests.

2.2.4 Transmission between ant hosts

Successful transmission between ant hosts, both within and between colonies, is crucial to the fitness of parasitic organisms. For some, such as viruses, the process is comparatively simple and straightforward: have an infected individual come into contact with a susceptible individual. For other parasites, such as trematodes, life cycles involving multiple host species in different habitats make things a bit more complicated. To find large-scale patterns in records of parasites and parasitoids infecting ants, we define transmission by two major criteria: (i) whether multiple hosts are needed for the parasite life cycle and (ii) whether the parasite must leave the nest before transmission can occur (Fig. 2.2). In cases of indirect transmission, parasitic organisms need more than one host in order to complete their life cycle. In many cases, this indirect transmission strategy relies upon trophic transmission, in which parasitic organisms are transmitted between hosts when one susceptible host consumes an infected host [177] (Fig. 2.2).

Transmission can be further defined by whether a parasite is capable of transmitting directly inside the nest (*in-nido* transmission) or whether it needs to leave the nest in order to complete development prior to transmission to the next host (*ex-nido* transmission) (Fig. 2.2). While this distinction is specific to ants and other social insect colonies, it is crucial for the infection dynamics of these parasitic organisms (Chapters 3 and 4). For parasites that use indirect transmission strategies and thus multiple hosts, development outside the nest is required and thus *ex-nido* transmission naturally follows. For directly transmitting parasites, the distinction between *in-nido* and *ex-nido* transmission is crucially important. *In-nido* directly transmitting parasites, such as viruses, can infect one ant and be transmitted directly to another nest mate, creating the potential for intra-colony outbreaks. In contrast, *ex-nido* directly transmitting parasites (e.g. parasitoid wasps, zombie-ant fungi) infect one ant, must leave the nest to complete development (i.e. find a mate, develop sexual stages), and then must encounter and infect their next ant host. The time in which an *ex-nido* directly

transmitting parasite must spend outside the nest between hosts can vary widely, from days to over a year (Fig. 2.2), which has important implications for colony infection dynamics (Chapter 3).

2.2.5 Overarching questions and aims for this chapter

To understand the interconnected relationship of ants and their parasites we need a systematic and quantitative understanding of the parasites that are known to infect them. It has been 20 years since Paul Schmid-Hempel's monolithic work 'Parasites of Social Insects' [91], and in that time, much attention has been focused on uncovering mechanisms by which social insects might reduce intra-colony disease transmission (reviewed in [80, 97, 99, 127, 128]). While very important, we believe that such work needs to be grounded in the systematic understanding of parasites that infect social insects, their epidemiology and their natural history, and we further believe that parasites of ants merit their own review.

To that end, the major goal of this current work is to collect all extant records of parasitic organisms infecting ants, and from these records, synthesize major patterns in the natural history and epidemiological relationships of these parasites with their ant hosts. In so doing, we hope to begin to answer the following questions:

- Which parasite taxa most abundantly infect ants?
- Which encounter and transmission strategies predominate?
- Do certain parasite taxa assort with certain ant taxa?
- Are certain parasite or ant taxa undersampled?
- What are the epidemiological impacts of these parasites on ant colonies?
- How do infections at the level of the individual cascade up to impact colony survival or fitness?

While all of these questions will not be answered within this current work, collecting all ant-parasite records will move us forward to a point where such important questions can be begin to be addressed.

2.3 Methods

2.3.1 Defining an association record

In this study, we only consider the host at the individual level (colony member) and not at level of the whole colony (cf. [170]). In order to be as comprehensive as possible, we report all known associations of ants with their parasites and myrmecophiles, and to the extent that the biology is known, we report what that relationship is (i.e. parasite, parasitoid, nest associate, predator).

An association record consists of an instance of a parasite/myrmecophile genus (and species, if possible) associated with an ant genus (and species, if possible). For a given ant-parasite combination, multiple occurrences are possible, for example if the association is recorded from multiple locations, at multiple times, or by multiple collectors. However, we consider each ant-parasite combination as a singular ‘record’ regardless of how many times and places that association has been observed. For interested readers, we aim to provide references for each individual parasite-ant occurrence reported in the literature, but these are subsumed within a singular ant-parasite record (Appendix A).

Literature search

Records of parasites infecting ants were obtained by collecting all records within parasite-specific review papers and books [178–181], parasite-specific databases (the Universal Chalcidoidea database [182], the Strepsiptera database [183], the Phorid catalog [184], and the USDA nematode collection, [185]), host-specific books ([22,91]), by executing a targeted search for all genera within the ants, and through serendipitous discovery. The targeted search was carried out by systematically searching for each extant, recognized ant genus [7] and the term par* within the CAB abstracts database (www.cabi.org), which provides access to English-language translation of abstracts and papers which are in foreign languages and as such often not available in more commonly employed databases (e.g. Web of Knowledge). In addition to both extant databases and the targeted ant genus search, serendipitous discoveries of ant-parasite occurrences were also made, often buried deep within old texts. It is likely that some records have inevitably been missed, but we are confident that the majority of published records have been included in this work. A schema for how the literature search

was conducted is given in Fig. 2.3.

Updating parasite records

Many parasites infecting ants were first recorded many decades, even centuries, ago. In order to ensure that the parasite and host taxonomy details reported in records were up-to-date, parasite taxa were cross-referenced using the Catalogue of Life taxon database [186] and ant taxa were cross-referenced with currently recognized ant taxa [7]. In cases where either the parasite or ant taxa needed to be updated, we report the updated names in our records, but note the original names used in the reporting references in the ‘Comments’ section of our database, which will be made available upon publication of this chapter as a separate manuscript.

2.3.2 Categorizing parasite life history and epidemiological features

In order to understand how parasites could potentially impact ant colony functioning, relevant life history traits were scored for each parasite found to be associated with ants. We focus on three essential epidemiological characteristics: encounter (how the parasite encounters hosts that it can infect, Fig. 2.1), virulence (morbidity or mortality for individual ants), and transmission (number of hosts in life cycle and whether the entire life cycle can occur within the confines of the ant nest). Additionally, we report the ant life stage infected (i.e. brood vs. adult, worker vs. queen) if known, and categorize the relationship of the parasite and the ant according to the definitions previously discussed. Below we provide details for how parasites were characterized. The database of parasite records along with selected parasite traits is given in Appendix A; we will provide a complete and searchable database upon publication of this chapter as a separate manuscript.

2.4 Results: parasite-specific

We report 2,020 records of associates of ants. These records comprise 104 unique associate families, 336 unique associate genera and 977 unique associate species associated with 88 ant genera and 674 ant species. A fully searchable database of

all associate records and their relevant life history traits will be made available upon publication.

Of these reported associates, parasitoidism is the predominant relationship with the ant host (62.7%, 1267/2,020 records), followed by general association (23.8%, 480/2,020 records), parasitism (7.3%, 148/2,020 records), predation (5.7%, 116/2,020 records), and hyperparasitism (0.4%, 9/2,020 records) (Fig. 2.3). Since the primary focus of this work and literature search was on parasites and parasitoids, the number of general associate records reported here is likely a vast underestimate of the number of organisms that are truly associated with ants. The rest of the results reported below pertain only to those records in which the relationship of the organism to the ant host is that of parasite or parasitoid.

2.4.1 Overall parasite life history trends

We report 1,415 records of parasitic organisms (parasites and parasitoids, hereafter 'parasites' when discussed generally) infecting ants, comprising 51 families, 160 genera, and 616 species infecting 81 ant genera and 580 ant species (Fig. 2.5). Below we summarize general trends in life history traits of parasites infecting ants and in Figures 2.6 - 2.10, we show how these traits assort across the major parasite groups. In Table 2.2 we summarize the number of parasite records, the unique parasite genera and species, and unique ant genera and species associated with each parasite family. In Table 2.3, we summarize the percentage of parasite records with a given life history trait (e.g. direct transmission) for each parasite family.

Parasitoidism, in which the death of the ant host is required as a developmental necessity, predominates, accounting for 89.5% of reported records (1,267/1,415) (Fig. 2.6). In contrast, parasitism, in which the death of the host is not required as a developmental necessity, accounts for only 10.5% of the reported records (148/1,415). In order to infect ant hosts, the majority of parasitic organisms use primary encounters (68.6%, 970/1,415 records, Fig. 2.7), wherein ants encounter parasitic organisms in the extranidal environment and subsequently become infected. 6.9% use secondary encounters (97/1,415 records), in which parasitic organisms encounter ants in the extranidal environment, become phoretically attached, and are carried inside the nest where they subsequently infect other individuals. 10.2% use independent encounters (144/1,415 records), meaning that the parasitic organism actively enters the ant nest on

their own. 13.9% use multiple means of encountering their hosts (196/1,415 records), and for 0.6% of parasite records it remains unknown how they encounter their hosts (8/1,415 records).

Most parasitic organisms infecting ants use direct transmission (only a single host is needed to complete life cycle) comprising 89.1% of the reported records (1,261/1,415 records, Fig. 2.8). In contrast, a smaller proportion use indirect (multi-host) life cycles, and these parasites are found within the Trematoda, Cestoda, and Nematoda (10.9%, 154/1,415, Fig. 2.8). The vast majority of parasites and parasitoids infecting ants use *ex-nido* transmission, which requires leaving the nest for a period of time before transmission to next ant host can occur (88.3%, 1,249/1,415 records, Fig. 2.9). *Ex-nido* transmission is found within the fungi, worms, and insects, but is absent from viruses, bacteria, microsporidia, and apicomplexa (Fig. 2.9). Finally, the majority of parasites and parasitoids infecting ants develop internally inside the host as endoparasites (84.2%, 1,191/1,415 records, Fig. 2.10). We plot the co-association of relationship to the host (parasite or parasitoid) and transmission location (*in-nido* vs. *ex-nido* in Fig. 2.11).

2.4.2 Viruses

[15 total association records | 15 parasite records]

Knowledge of viruses infecting ants is quite limited, largely due to the relative difficulty in isolating and identifying viruses compared to other taxa and due to the inherent difficulties in observing and sampling dead or dying ant hosts, particularly in natural field settings. At least 18 viruses are known to infect genera within the Apidae [91, 187–190], but our knowledge of viruses potentially infecting the Formicidae is just beginning to catch up. The first reports of potential viral infections in ants were by Steiger et al. [191], who found ‘virus-like’ particles infecting *Formica lugubris* and Avery et al. [192], who found ‘virus-like’ particles infecting an unidentified *Solenopsis* species, but the first confirmed report did not occur until 2004.

Single-strand RNA viruses (ssRNA+)

Valles et al. [193] report the first confirmed instance of a virus infecting ants, *Solenopsis invicta* virus-1 (SINV-1). Subsequent work has found SINV-1 infecting *S. invicta* colonies in both Argentina and the United States [194, 195]. The virus has been found

infecting other species within the *Solenopsis* genus (*S. geminata*, *S. richteri*, and *S. carolinensis*, as well as some *Solenopsis* species hybrids, [196]). While SINV-1 has been detected in ants, its actual host pathology remains unclear. Valles et al. [193] note no observable symptoms of virus infection in natural populations, but did note virus-induced larval mortality in the lab. While the virus appears to have a limited impact on individual hosts, it does appear that its presence may alter the competitive ability of infected colonies. When competed against colonies of other species, SINV-1 infected colonies of *S. invicta* were weaker competitors compared to their uninfected counterparts [197].

Shortly after the discovery of SINV-1, two other related viruses, SINV-2 and SINV-3, were found to infect *Solenopsis invicta* [194, 198]. There is little evidence that SINV-2 causes any observable host pathology and its host specificity remains unknown (Valles 2012), as does its taxonomic placement. Allen, Valles, and Strong [199] report finding co-infections of various combinations of SINV-1, SINV-2, and SINV-3 in individuals of *Solenopsis invicta* colonies, with polygyne colonies having a higher virus prevalence. It is unknown how having multiple viral infections impacts the morbidity and mortality of individual ants, or how the presence of multiple viruses affects colony-level functioning.

In contrast, SINV-3 has been shown to cause considerable mortality in laboratory colonies of *S. invicta*, particularly among brood [198]. Further studies have shown that SINV-3 can negatively impact queen egg production and brood development [200], perhaps due to behavioral changes caused by the virus that impede the ability of workers to disseminate food within the colony [201]. In some cases, SINV-3 infected colonies have been shown to rebound following the initial infection period [196], but SINV-3 remains the most pathogenic virus known to infect ants.

Celle et al. [202] report Chronic Bee Paralysis virus (CBPV) from *Camponotus vagus* and *Formica rufa*. This virus was isolated from these hosts due to their proximity to infected beehives and not because there were signs of virus-induced pathology to the ants. While these ants may become infected by the virus, the effects of CBPV on ant health and any transmission potential inside ant nests remains unknown.

Gruber et al. [203] conducted an extensive survey for viruses of the invasive Argentine ant *Linepithema humile* in New Zealand. They found a novel ant-specific virus *Linepithema humile* virus-1, as well as several viruses normally found in bees: Kashmir bee virus (KBV), black queen cell virus (BQCV), and deformed wing virus (DWV). The

pathology of these viruses on their ant hosts is not noted, only their presence. Gruber et al. [203] comment on the potential role of ants as reservoirs for viral disease in the presence of apiaries:

‘We found that viral load of both DWV and KBV was also higher in Argentine ants when these ants were interacting with bees: markedly so for DWV, with viral concentrations five orders of magnitude higher when the ants were present in honey bee apiaries. These viruses were also present at all other sites, including in urban areas where there were no bee hives with several hundred meters of the sample collection location. Viruses such as DWV, KBV and BQCV are clearly present in these invasive ants in the absence of close contact with bees.’

Single-strand DNA viruses (ssDNA +/-)

Valles et al. [204] report the first DNA virus from a hymenoptera host, *Solenopsis invicta* densovirus (SiDNV) infecting *S. invicta* in Argentina. Despite extensive sampling of *S. invicta* colonies in the United States where the ant is invasive, the virus was not detected there, suggesting that the virus might be a promising tool for biocontrol of the pestiferous ant species. It is unclear to what extent the virus impacts individual ant morbidity or mortality.

Records of viruses infecting ants

[15 association records, 6 parasite records]

We report 9 known viruses infecting ants (SINV-1, SINV-2, SINV-3, SiDNV, LHUV-1, KBV, DWV, BQCV, and CBPV, Table 2.2), representing 6 virus families. There is a wide range in the pathogenicity of the reported viruses, ranging from no observable symptoms to host mortality only in the case of SINV-3. Thus far, only 7 ant species (and 2 hybrid *Solenopsis* species) have been identified as hosts. This is certainly an underestimate of the number of viruses infecting ants and an underestimate of the number of ant species infected, and the numbers will grow as more surveys explicitly looking for viral pathogens are performed.

2.4.3 Bacteria

[141 total association records | 1 parasite record]

Reports of bacteria associated with ants have become more prevalent over the past few decades, as improved molecular methods have allowed for the identification of bacteria species previously unculturable or unidentifiable in the lab. Several surveys have looked for bacterial pathogens and associates within ant colonies [205–209], often for purposes of identifying potential biocontrol agents. However, in the majority of these surveys, the exact association between the bacteria and the ant host (i.e. mutualistic, pathogenic, or somewhere in between) remains unknown.

Lofgren et al. [210] report that a *Pseudomonas* bacteria was found in dead ants taken from *Solenopsis* colonies in Mississippi, USA. When cultured and fed to ants in the lab, the bacterium readily killed all larvae and 50% of the adult workers. However, it is unclear whether this bacteria was the causative agent of death in the dead ants they initially isolated from the nest mounds, or whether *Pseudomonas* colonized these dying/dead ants opportunistically. While mortality was observed in the lab, it is unclear whether the infective dose used represents a biologically reasonable dose. Jouvenaz et al. [205] conducted a wide survey of bacterial and microsporidian pathogens associated with *Solenopsis invicta* and *S. richteri* in their native range in Brazil. Out of 640 colonies sampled in their surveys, a few larvae in only 1 colony were found to harbor a ‘sporeforming bacterium’ [205]. Attempts to isolate the bacterium were unsuccessful, so its transmission and pathogenicity could not be determined.

More recently, surveys looking for ant microbial associates have identified many bacteria in the environment in and around ant nests. Baird et al. [206] found 58 bacterial isolates associated with *Solenopsis* mound soil, mound plant debris, and on the external body regions of ants. Ishak et al. [207], Powell et al. [208], and Woolfolk et al. [209] performed follow-up studies, finding bacterial isolates from *Solenopsis invicta* and *Solenopsis geminata* mound soil, surrounding plant debris, and internal and external ant tissues.

Bacteria as endosymbionts and mutualists

Much work is currently being devoted to understanding the diversity of bacteria within ant colonies and the role that they provide as endosymbionts and mutualists [19, 47, 207, 211–213]. Obligate endosymbionts, such as *Blochmannia* [214] and *Wolbachia*

[211], have long co-evolutionary histories with their ant hosts and have been linked to the evolution of herbivory in the ants [19], and may be extremely important for the nutritional ecology of different ant species [215]. Other bacteria species may play an important role in preventing colony infection by other pathogens and parasites (Little et al. 2006, Mattoso et al. 2011). How ants and other social insects differentiate between their endosymbiotic bacteria and those that are pathogenic is an interesting and open question [216], as is how these relationships evolve over time [47].

Records of bacteria infecting ants

[1 parasite record]

Associates, mutualists, and endosymbionts of ants are outside the scope of this present work. For interested readers, we present a non-exhaustive list of recorded bacterial associates that have unclear relationships with their ant hosts. From these records, we report 104 species of bacteria (representing 72 genera in 48 families) as associates of ants (Appendix A, Table A.2). These bacteria are associated with 4 species of ants: *Formica cinerea*, *Solenopsis geminata*, *Solenopsis invicta*, and *Solenopsis sp.* This non-exhaustive list can certainly be expected to grow as more molecular surveys are conducted and more ant species are surveyed.

Importantly, we only report a single case where a bacterium is known to cause host morbidity or mortality, though this is only known from laboratory experiments (*Pseudomonas sp.* infecting *Solenopsis sp.* - [210], Table 2.2). While we should continue surveying the diversity of microbes associated with ant colonies, understanding their ecological interactions with their hosts remains an important goal. The ecological interactions of these bacteria are likely to be more complex than anticipated and potentially pathogenic bacteria might only reveal themselves as such under the right conditions. For example, bacterial pathogens known to infect bees (Hymenoptera: Apidae) often act as secondary invaders, associated with infestation by *Varroa* mites or with other infections that might make hosts more vulnerable [91]. Bacteria that are symbionts of other taxa might become pathogenic to ants under specific conditions: the dauer stages of facultatively entomopathogenic nematodes can enter openings in ant hosts, and after a period of quiescence can rupture host membranes, allowing their symbiotic bacteria to kill the ant host [217].

While our catalog of bacteria associated with ants continues to grow, our under-

standing of their interactions over ecological and evolutionary time remains limited but testable [47] and is ripe for future work.

2.4.4 Fungi

[419 total association records | 362 parasite records]

Ants have a long evolutionary history with fungi [17, 218, 219]. The symbiosis between leaf-cutter ants and their fungi dates back at least 50 million years ago [17, 219–221], and records of ant parasitism by fungi have been preserved in leaf fossils from 48 million years ago [222]. The ecological interactions between ants and fungi are diverse, ranging from mutualism (e.g. between leaf-cutting ants and their cultivated fungi), to facultative parasitism (e.g. by generalist entomopathogens) and parasitoidism (e.g. by the zombie ant fungus *Ophiocordyceps*), and all shades in between.

Fungi as pathogens and parasites of ants

The diversity and pathology of fungi infecting insects has been extensively reviewed in the literature [218, 223–227]. It is outside the scope of this present work to review the fungal biology involved; here we provide a brief overview of each family of fungi recorded infecting individual ants and the records thereof. We do not include records of fungi found in or around ant colonies (e.g. fungi isolated from soil or leaf litter near colonies, from colony refuse piles, or from ant fungal farms), nor do we include records where fungi have been isolated from ant external surfaces without indication of pathology. Interested readers are referred to Baird et al. [206], Reber and Chapuisat [107], Woolfolk et al. [228] and references therein for surveys of fungi generally associated with ant colonies. We present our records of fungi known to infect ants in Appendix A, Table A.1.

Fungal epidemics in ant colonies are rarely reported in the literature (reviewed by [91, 224, 225, 229]). As Espadaler and Santamaria [225] note in their review of ecto- and endoparasite fungi of ants: “Extensive, massive mycoses are an extremely rare instance in ants [5] and involve individuals, rather than whole colonies”. Evans [230] notes: “Fungal pathogens of ants and other arthropods have been regularly collected from Ghanaian cocoa farms (H.C. Evans, unpublished) but epizootics are of infrequent occurrence and disease is at an enzootic level”. Many fungi have been isolated from in and around ant colonies [107, 206] and from ant internal tissues [228], often for

the purposes of identifying potential biocontrol agents, but these have not been accompanied by any observations of colony collapse due to disease. Indeed, in a long-term study monitoring colonies infected by the behaviorally-manipulating fungus *Ophiocordyceps unilateralis* in the field, Loreto et al. [231] note that all 17 surveyed colonies continued to function over the 20-month observational period despite the chronic infection by a fungal disease.

The absence of fungal disease epizootics in natural ant populations contrasts starkly to the reported impacts of fungal disease on ant colonies in laboratory settings, where generalist fungal pathogens in the genera *Metarhizium* and *Beauveria* are routinely used to investigate potential mechanisms of social immunity (reviewed in [232]). Large infective doses and the use of fungal pathogens which are not naturally co-evolved with ants might explain the discrepancy between fungal-induced mortality in the lab and the paucity thereof in the field [232].

Records of fungi infecting ants

We report 362 records of parasitic fungi (16 families, 40 genera, 115 species) infecting 238 ant species. These fungi come from two phyla (Ascomycota and Zygomycota) and 9 orders (Capnodiales, Entomophthorales, Eurotiales, Hypocreales, Laboulbeniales, Mucorales, Ophiostomatales, Pleosporales, Saccharomycetales).

Ancylistaceae (Zygomycota: Order Entomophthorales)

[1 total associate record | 1 parasite record]

One species of fungi in the family Ancylistaceae has been found to parasitize ants (*Conidiobolus* infecting *Solenopsis invicta*, Sanchez-Pena and Thorvilson 1992). *Conidiobolus* is a pathogen of termites [233, 234] and aphids and very occasionally infects vertebrates [235]. In the case of ants, *Conidiobolus* was recorded from 3 out of approximately 1,000 samples of red imported fire ant queens that had recently completed their mating flight [236].

Entomophthoraceae (Zygomycota: Order Entomophthorales)

[13 total associate records | 13 parasite records]

We report the genera *Tarichium* and *Pandora* as the only Entomophthoraceae fungi known to infect ants.

Tarichium has only been reported from ants once (infecting *Tetramorium caespitum* in Russia, [237]), but it is an intriguing record as it appears to have caused a “dying out of a large number of this species”. Marikovskiy [237] notes that healthy ants began emigrating from their infected colonies, perhaps to escape parasite pressure. No other reports of *Tarichium* infecting ants have been observed, nor have other outbreaks killing off whole colonies. The details on the relationship and prevalence of *Tarichium* infecting ants are unfortunately scarce, and follow-up work is needed to confirm the veracity of the fungal identity. Due to the similarities in the biology of *Tarichium* and fungi in the genus *Pandora* (Ophiocordycipitaceae), this record likely belongs in the genus *Pandora* (see taxonomic review in [238]).

Pandora (12 records) is reported parasitizing ants exclusively from the genus *Formica* in Europe (reviewed within [239]). The genus currently consists of two species, *Pandora formicae* and *Pandora myrmecophaga*, though their status as separate species is unclear (see taxonomic review in [238]). This fungus causes the characteristic symptoms of summit disease (well-described in [237, 240]). As noted by Malagocka et al. [238] and observed in other specialized fungal entomopathogens [231, 241], the fungus is unlikely to sporulate inside the nest, and must grow and therefore be transmitted outside of ant colonies.

Cunninghamellaceae (Zygomycota: Order Mucorales)

[3 total associate records | 0 parasite records]

3 records of Cunninghamiellaceae representing 2 genera, *Cunninghamella* and *Absidia*, are associated with the ant species *Paratrechina longicornis* [242]. These fungi were isolated from recently dead ant cadavers, and it is unknown whether they killed the ant or were members of the ant microbial community that became opportunistic invaders following host death.

Davidiellaceae (Ascomycota: Order Capnodiales)

[1 total associate record | 0 parasite records]

Cladosporium sp. is associated with *Paratrechina longicornis* in Brazil [242]. The fungus was isolated from ant cadavers following death, thus it is unclear whether this

fungus, which is likely a member of the ant microbial community, was the cause of death or instead an opportunistic invader.

Ophiostomataceae (Ascomycota: Order Ophiostomatales)

[3 total associate records | 0 parasite records]

Sporothrix insectorum has been reported from *Crematogaster*, *Macromischoides*, and *Paltothyreus* in Ghana ([230, 243], reviewed in [224]). Its effects on host morbidity or mortality are unknown.

Plectosphaerellaceae (Ascomycota: Order Incertae Sedis)

[3 total associate records | 0 parasite records]

A single species of this family, *Verticillium nodulosum*, has been recorded from *Dorylus*, *Macromischoides*, and *Paltothyreus* in Ghana ([230], reviewed in [224]). Its effects on host morbidity or mortality are unknown.

Endomycetaceae (Ascomycota: Order Saccharomycetales)

[1 total associate record | 0 parasite records]

Geotrichum sp. is associated with *Paratrechina longicornis* in Brazil [242]. The fungus was isolated from ant cadavers following death, but it is unclear whether the fungus, which is likely a member of the ant microbial community, was the cause of death or instead an opportunistic invader.

Trichocomaceae (Ascomycota: Order Eurotiales)

[22 total associate records | 8 parasite records]

Generalist fungi in the family Trichocomaceae belonging to the genera *Aspergillus*, *Neosartorya*, *Paecilomyces*, *Penicillium*, and *Petromyces* have been recorded infecting ants. The majority of these records are for ants in the genera *Solenopsis* and *Paratrechina*, where targeted surveys have actively searched for fungal pathogens as potential use as biocontrol agents against these pestiferous genera [228, 242]. Other ant genera infected include *Formica* and *Atta*.

For several of these records, the fungus was isolated from ant internal tissues in the absence of ants exhibiting any pathological symptoms (i.e. records within [228]),

so the morbidity and mortality caused by these fungi remains unknown. Other fungi within this family have been demonstrated to infect and kill their ant hosts (i.e. species listed within Fernandez-Marin et al. 2006, Rodrigues et al. 2010); however, these were laboratory infections and there are no records of colonies naturally infected by these fungi in the field. Evans [224] notes that *Aspergillus* and *Penicillium* have been associated with moribund ants, but considers them to be “opportunistic pathogens on damaged or stressed ants”.

Pleosporaceae (Ascomycota: Order Pleosporales)

[3 total associate records | 1 parasite record]

Three genera of fungi from the Pleosporaceae are associated with ant hosts: *Alternaria*, *Cochiobolus*, and *Curvularia*. Two of these fungi, *Cochiobolus*, and *Curvularia*, have been isolated from ant internal tissues in the absence of any pathological symptoms [228], so their association with ants remains unknown. Although unknown, these pathogens would presumably be able to spread directly between ant hosts inside the colony.

Alternaria tenuis infecting *Formica rufa* [237] is an *ex-nido* transmitting fungal parasite, requiring the death of its ant host outside of the nest in order to be able to develop and properly transmit. Marikovsky (1962) deftly describes the suite of behavioral changes that infected ants undergo, collectively referred to as “summit disease”, writing:

‘A few hours before death the infected ant would appear in a very good health, it could move about normally and even quite vigorously. It would also defend itself if attacked. It would emerge out from the nest and climb on the very tip of a low grass blade. As a rule, diseased ants chose the grass from 10 to 30 cm high, which would be necessarily in the vicinity of the ant-hill, or on the mound range. [...] After inspecting the grass blade for some time the diseased ant clings fast to it with its mandibles. [...] After being fixed the ants died very quickly. In the morning of the second day on the body of a dead ant in the intersegment folds there appeared narrow stripes of dazzling white fungus mycelia, which grew through the ant’s body. [...] Ants covered with conidia were the source of infection in other ants.’

Marikovskiy reports that disease due to *Alternaria* occurred primarily in the late summer or early fall, and that fungal development on the outside of the host, and thus onward transmission, was prevented if the death of the host occurred on a particularly dry or sunny days. Evans (2001) notes that the identification of the fungus as *Alternaria* might be doubtful, because “*A. tenuis* is a common saprophyte and has no previous or present history as an entomopathogen. Indeed, the host and the description of the behaviour and habitat suggest that the true pathogen is in fact a member of the Entomophthoraceae [244] and that *A. tenuis* is an opportunistic invader, possibly outcompeting the primary pathogen.” [224].

Laboulbeniaceae (Ascomycota: Order Laboulbeniales)

[39 total association records | parasite records]

We report 39 records of fungi from the family Laboulbeniaceae associated with ants. These records represent only 2 genera, *Laboulbenia* and *Rickia*, primarily infecting the ant genera *Formica*, *Lasius*, and *Camponotus* in Europe and the United States.

The biology and host records of *Laboulbenia* and *Rickia* are reviewed in Espadaler and Santamaria (2012); both fungi are obligate ectoparasites, growing on the cuticle of ants without appearing to harm the host [225]. Workers and queens have been found to be infested by these fungi, and transmission is presumably accomplished by direct contact with fungal material between nest mates. Evans (2001) notes that the Laboulbeniaceae have never been implicated in host mortality and are “commensal parasites” of ants. In our database, we note them as parasites, but clearly more studies are needed to determine their impact on individual ant health.

Hypocreaceae (Ascomycota: Order Hypocreales)

[4 total association records | 0 parasite records]

3 genera within the Hypocreaceae are associated with ants: *Acremonium*, *Hypocrea*, and *Trichoderma*. Both records for *Acremonium* were isolated from dead ant cadavers, therefore it is unknown whether the fungus was the causative agent of ant mortality. The record for *Hypocrea* was found by surveying for microbial associates in ant internal tissues [228], and the ants sampled did not display any signs of pathology. Thus, for both *Acremonium* and *Hypocrea*, the exact relationship with ant hosts remains unclear.

Trichoderma is reported from a recently mated *Atta* queen, who was collected

following her mating flight and held in the lab until death [242]. *Trichoderma* was isolated from the ant cadaver, but it is unclear whether it was the causative agent of death, or a secondary or opportunistic infection following death.

Nectriaceae (Ascomycota: Order Hypocreales)

[5 total association records | 0 parasite records]

We report 5 records of fungi from the family Nectriaceae associated with ants, all from the genus *Fusarium*. *Fusarium* is a large genus of plant pathogenic fungi, normally found in soil, whose members are largely saprophytic [245]. Some *Fusarium* species have been shown to cause disease in other insect species [246], but this has not been previously reported infecting ants or any other Hymenoptera.

The records of *Fusarium* associated with *Solenopsis invicta* were obtained from the internal tissues of ants that did not show any signs of pathology [228], so whether *Fusarium* is a non-pathogenic member of the ant microbial community or is truly pathogenic is unknown. The lack of reports from other ant species and its relatively wide abundance in soil communities makes *Fusarium* unlikely to be a pathogen of ants under ordinary circumstances. The reports of *Fusarium* associated with *Atta* were collected from recently mated alates who were held in the laboratory without food until death, at which time the corpses were observed for signs of entomopathogenic fungi [242]. It is unknown whether the *Fusarium* species isolated from the *Atta* cadavers were the causative agent of death, or whether they were present as opportunistic saprobes following host death.

Clavicipitaceae (Ascomycota: Order Hypocreales)

[7 records]

Metarhizium is the only genus of fungi within the Clavicipitaceae reported to infect ants. This generalist fungus requires the death of its insect host; following death, hyphae emerge from the insect body and sporulate, and transmission occurs via direct contact with spores. This genus is incredibly cosmopolitan, infecting many species of insects [247], and it appears to be an important part of the soil microbial community.

While this fungus is used extensively in the laboratory to investigate mechanisms of ant social immunity (reviewed by [232]) and despite its wide distribution in soil microbial communities [248], it has been rarely reported infecting ants in natural

populations (reviewed in [224]). The first recorded instance of *Metarhizium* infecting an ant is from Petch [249], who noted it infecting a “black ant”. It has since been reported from *Atta*, *Formica*, *Leptogenys*, *Paratrechina*, and *Solenopsis*. There are no reports of ant colony epizootics due to *Metarhizium* in natural populations.

Cordycipitaceae (Ascomycota: Order Hypocreales)

[46 total association records | 31 parasite records]

The Cordycipitaceae were previously grouped within the Clavicipitaceae; revision by Sung et al. (2007) instated the Cordycipitaceae as its own family [250]. 2 genera within the Cordycipitaceae are known as parasites of ant hosts: *Akanthomyces* and *Beauveria*.

Akanthomyces gracilis is reported from *Camponotus*, *Crematogaster Dorylus*, *Macromischoides*, *Oecophylla*, *Paltothyreus*, *Platythyrea*, and *Polyrhachis* (reviewed in [224]). Evans (2001) notes that when dead insects infected by this fungus are hidden in the soil or leaf litter, they bear long synnemata “which ramify above or within the substrate”. However, it is unclear whether *Akanthomyces* is the causative agent of host death, or merely an opportunistic hyperparasite (Araujo, personal communication). Additional studies are needed to ascertain its relationship to the ant host.

Beauveria has been found to naturally infect over 700 insect species and has been used prolifically for the purposes of biocontrol (reviewed in [251, 252]). *Beauveria* has recently been found to be paraphyletic [253], so though we report a single species, *Beauveria bassiana*, infecting ants, we can expect additional records as the diversity within *Beauveria* is unraveled. *Beauveria bassiana* has been found infecting ants in the genera *Atta*, *Camponotus*, *Cephalotes*, *Crematogaster*, *Ectatomma*, *Formica*, *Lasius*, *Myrmecia*, *Oecophylla*, *Paraponera*, and *Solenopsis*. Like *Metarhizium*, *Beauveria* has been used as a laboratory workhorse to understand potential mechanisms of social immunity in ant colonies [232]. Epizootics due to *Beauveria* in natural ant populations are unreported.

Ophiocordycipitaceae (Ascomycota: Order Hypocreales)

[202 total associate records | 197 parasite records]

The majority of records of fungi infecting ants come from the Ophiocordycipitaceae. Prior to its re-erection in 2007, members of the Ophiocordycipitaceae had

been placed within the polyphyletic family Clavicipitaceae. The Ophiocordycipitaceae contains the striking “zombie ant” fungus *Ophiocordyceps*, known for the sophisticated and species-specific behavioral manipulation of its host [241, 254–258]. Prior to the adoption of the “One Fungus, One Name” policy [259], the genera *Hirsutella*, *Hymenostilbe*, *Stillbella*, and *Stilbum* were also included in this family, but these are asexual stages (=anamorphs) of *Ophiocordyceps* and thus are no longer used. Other genera infecting ants in this family are *Paraisaria* and *Polycephalomyces*.

Ophiocordyceps is an old genus that had been moved within *Cordyceps* but was re-erected following the major revision of the Clavicipitaceae [250]. There has been much focus on this genus in recent years, with many new species being described from former species complexes [258, 260, 261]. These species complexes, including: *O. unilateralis*, *O. australis*, *O. kniphofioides*, *O. myrmecophila*, and *O. sphecocephala*, undoubtedly contain many new species awaiting description. With the exception of *O. sphecocephala*, all are parasitic on ants.

Incertae Sedis

[66 total association records | 65 parasite records]

4 genera of fungi infecting ants are currently without family-level placement: *Aerigitella*, *Hormiscium*, *Myrmecomyces*, and *Mymicinosporidium*.

Aerigitella (23 records) is an ectoparasitic fungus known primarily from *Formica* and *Lasius* in Europe and the United States [225]. As reviewed by Espadaler and Santamaria (2012), the relationship of this fungus with its ant host, its life history, and mode of transmission are unknown. Some suggestions that it might cause reduced life span or activity have been noted [262, 263].

Hormiscium (3 records) is an ectoparasitic fungus described from *Pseudomyrmex* and *Myrmica* in South America and Europe, respectively (reviewed in [225]). Little information is known about its biology and relationship to its ant host.

Myrmecomyces (1 record) is reported infecting *Solenopsis* ([264], within [224]). Its effects on host morbidity and mortality are unknown.

Mymicinosporidium durum (39 records) is an endoparasitic fungus of uncertain phylogenetic position that has been found infecting many different ant genera and species ([265–268], reviewed in [225]). Though first described in the 1920’s [269, 270], the life-history of the fungus remains unknown, and it is unclear what the effect of

infection does to the ant host in terms of either morbidity or mortality [225, 236]. Sanchez-Pena et al. (1993) note that the fungus “does not seem to impair significantly the mobility or behavior of the ant hosts, despite extensive vegetative development and sporulation prior to host death”. There has been discussion over whether *Myrmicinosporidium* might be a single generalist species [268], or whether it could constitute a fungal complex with many new species awaiting description [225, 266]. The enigmatic life history and host relationship of this fungus, coupled with its wide host range and geographic distribution make this fungus ripe for future work.

2.4.5 Microsporidia and Apicomplexa

[13 total association records | 13 parasite records]

Microsporidia are a group of obligate, unicellular, spore-forming parasites [271]. Formerly grouped within the protozoans, the Microsporidia have been found to be closely related to fungi [272], though their larger taxonomic placement (i.e. within the fungi or as a sister group to fungi) remains uncertain. One family within the Microsporidia, Burenellidae, has been recorded infecting ants from the genus *Solenopsis*, though some parasites in the group are awaiting family-level placement.

Microsporidia: Burenellidae

[5 records]

Two genera within the Burenellidae, *Burenella* and *Vairimorpha*, have been found infecting ants in the genus *Solenopsis* in South America. *Burenella dimorpha* was first described by Jouvenaz and Hazard (1978) infecting the fire ant *Solenopsis geminata* [273]. As noted by those authors, host pathology is only observed in pupae, and infected pupa have been observed being cannibalized in the laboratory [274]. Transmission experiments show that the parasite is transmitted to 4th-instar larvae per os by workers tending brood [273, 274]. Adults don't seem to become infected because they are able to filter out infective spores in their infrabuccal pocket [274].

Vairimorpha is a closely related genus also found infecting *Solenopsis*. Unlike *Burenella*, Jouvenaz and Ellis (1986) found that all ant stages of *S. invicta* (i.e. brood and adults) could be infected, but do not report any physical or behavioral symptoms associated with infection [275]. Briano et al. (2002) surveyed many ant genera for the presence of microsporidians, but only report finding *Vairimorpha*-infected *Solenopsis*

(*S. invicta*, *S. macdonaghi*, and *S. richerti*) at low prevalences [276].

Microsporidia: *Incertae Sedis*

[4 total association records | 4 parasite records]

Kneallhazia solenopsae (formerly *Thelohania solenopsae*, in the family Thelohaniidae) was first described from *Solenopsis invicta* in Brazil [277]. Surveys have found it to be the most common microsporidian parasite infecting fire ants in South America [274, 276, 278, 279], and it has also been found parasitizing some *S. invicta* colonies in the southeastern United States [280]. Sokolova and Fuxa (2008) found that spores can be transmitted both transovarially and per os through trophallaxis, infecting all stages from brood to adults [281]. In both brood and adults, infection related pathology is inapparent [281], though Allen and Buren (1974) noted that infected colonies had a “noticeable loss of vigor and pursuit when disturbed” [277].

Apicomplexa: Lipotrophidae

[4 total association records | 4 parasite records]

One genus from the Apicomplexa, *Mattesia*, is recorded infecting species of *Solenopsis* in Brazil and the United States [205, 282]. Infections by *Mattesia* are apparent in brood, which eventually become almost solid black in coloration and do not complete their development [283]. Infected adult ants have not been observed [282–284], perhaps due to the filtering of infective spores through their infrabuccal pocket.

2.4.6 Trematoda

[21 total association records | 21 parasite records]

Trematodes (‘flukes’, phylum Platyhelminthes) are a class of flatworms with a wide diversity of free-living and parasitic lifestyles [285]. Parasitic trematodes use multi-host life cycles involving two to three hosts [285–287], in which molluscs serve as the first intermediate hosts and vertebrates serve as final hosts. Trematodes infecting ants are few but spectacular, and trematodes from two families, the Dicrocoelidae and the Heterophyidae, are recorded infecting ants. In these instances, the ants serve as second intermediate hosts in the multi-host life cycles of these trematodes. We report 21 records of trematodes from 2 families infecting 5 genera of ants.

Dicrocoeliidae

[20 total association records | 20 parasite records]

Two genera, *Brachylecithum* and *Dicrocoelium* are reported infecting ants. *Brachylecithum* is reported from *Camponotus* in the United States [288, 289], and *Dicrocoelium* is reported infecting *Cataglyphis*, *Camponotus*, *Formica*, and *Lasius* in Europe and Asia (reviewed in [290]). The life cycle of both parasites is complex, involving snails as first intermediate hosts and vertebrates as final hosts, and it took over 100 years for the life cycle to be elucidated by Krull and Mapes (1952) [291]. Infected land snails produce slime balls containing trematode cercariae, which ants readily eat. The cercariae then penetrate the ant's crop (social stomach) and enter the hemocoel, where they migrate through the ant's body to the gaster and brain, forming metacercarial cysts [289]. Carney (1969) found that it could take as long as 120 days for the metacercarial cysts to develop and become infective [289]. Once the trematodes are ready to find their next host, infected ants display several behavioral changes that serve to increase the probability of trophic transmission to the next host. These behavioral changes include sluggishness, lack of sensitivity to light, and more time spent outside the nest (see description in [289]).

Heterophyidae

[1 total association record | 1 parasite record]

Eurytrema pancreaticum is reported infecting *Technomyrmex detorquens* [292]. The life cycle of this parasite is thought to be similar to that of dicrocoelid trematodes infecting ants, though due to the limited number of records, any behavioral changes in infected ants associated with this parasite are unknown.

2.4.7 Cestoda

[66 total association records | 66 parasite records]

We report 5 genera of cestodes in 3 families infecting 44 host species. Cestodes ('tapeworms', phylum Platyhelminthes) are a class of parasitic flatworms that typically live in the digestive tracts of vertebrate final hosts. Ants are intermediate hosts in the life cycles of several cestode genera from three families: Davaineidae, Dilepididae, and Mesocestoididae. Cestode-infected ants have been recorded primarily due the impact

that these tapeworms have on their final hosts (i.e. poultry and other domesticated animals, occasionally including humans).

Life cycles of cestode-infected ants are fairly straightforward: adult ants find cestode proglottids while foraging, and bring these proglottids back into the colony. Proglottids or oncospheres are fed to the brood, which then develop into cysticercoids or proceroids. When infected brood have matured into adults, they are behaviorally more sluggish than their non-infected counterparts, and thus more likely to be consumed by predators who act as second intermediate hosts or final hosts. Following reproduction in their final host, the final host deposits cestode-egg-laden feces, which are consumed by ants to begin the cycle anew.

Davaineidae

[62 total association records | 62 parasite records]

Davaineid cestodes from the genera *Cotugnia* (6 records) and *Raillietina* (56 records) have been recorded infecting ants. *Cotugnia digonopora* has been found infecting *Monomorium* and *Pheidole*. *Raillietina* (17 species) has been found to infect 14 ant genera in Africa, Asia, Australia, Europe, and North America.

Dilepididae

[2 total association records | 2 parasite records]

Anomotaenia brevis and *Choanotaenia crateriformis* have been recorded from *Lepthorax* in France and Spain.

Mesocestoididae

[2 total association records | 2 parasite records]

Mesocestoides has been occasionally reported infecting humans and domesticated animals, but the life cycle of this tapeworm has remained enigmatic for over a century. It has been thought that oribatid mites and other arthropods could serve as first intermediate hosts, but surveys for the tapeworm in these arthropods have been elusive. Very recently, ants (*Lasius niger* and *Tapinoma sessile*) have been identified as first intermediate hosts in the life cycle [293].

2.4.8 Nematoda

[68 total association records | 68 parasite records]

We report 68 records of parasitic nematodes comprising 10 families and 27 genera infecting 20 ant genera and 43 ant species. Nematodes ('roundworms') are a diverse phylum in which more than half of its members use a parasitic lifestyle [294, 295]. Parasitism has evolved at least 15 times independently within this phylum over the course of its evolutionary history [295]. Fossil evidence indicates that relationships between ants and nematodes date back at least 40 million years [296–298].

The biology, extant knowledge, and host records of nematode parasites of ants have been well reviewed by Poinar (2012) [298]. Here we report known records of nematodes associated with ants, and summarize some interesting aspects of their biology. A large number of nematodes in the family Rhabditidae are phoretically associated with ants, and the majority of nematodes infecting ants belong to the family Mermithidae.

Allantonematidae

[2 total associate records | 2 parasite records]

The Allantonematidae reported infecting ants comprise two genera: *Formicitylenchus* (extant) and *Paleoallantonema* (fossil). *Formicitylenchus oregonensis* is recorded from *Camponotus vicinus* in the United States [299]. Poinar (2012) notes that while many life cycle details remain unknown for this parasite, it is likely that free-living worms penetrate the cuticle of ant larvae and develop as the ant develops [298]. Poinar (2012) suggests that the nematode is spread by infected queen ants, but impacts on host behavior and morbidity or mortality are unknown. *Paleoallantonema cephalotae* is described infecting *Cephalotes serratus* from a fossil in Dominican amber [300], suggesting that the relationship between allantonematids and ants may be more widespread than what our current host records suggest [298].

Diplogastridae

[2 total associate records | 2 parasite records]

The Diplogastridae, along with the Rhabditidae and Panagrolaimidae, are families of nematodes in which the juvenile stages live phoretically with ants, either inside the pharyngeal glands or outside on the ant's cuticle. The damage to the host caused by

these associations is minor at best [298,301]. Within the Diplogastridae, *Formicodiplogaster myrmenema* (fossil) and *Pristionchus sp.* are recorded from *Azteca alpha* and *Atta cephalotes*, respectively.

Panagrolaimidae

[2 total associate records | 2 parasite records]

One genus in the Panagrolaimidae, *Panagrolaimus*, has been found infecting *Acromyrmex crassispinus* in Paraguay and *Atta cephalotes* in French Guiana [302]. Like the Rhabditidae and Diplogastridae, juvenile nematodes from this family are phoretic associates with ants causing minimal damage to their host [298]).

Rhabditidae

[29 total associate records | 29 parasite records]

The Rhabditidae, along with the Diplogastridae and Panagrolaimidae, are phoretic associates of ants that cause minimal damage to their host [298]. Many Rhabditidae live within the ant nest environs (see [302]), we only include those records that were isolated from ant bodies (either internal or external, head, body). 9 genera from the Rhabditidae, *Diplogasteroides*, *Diploscapter*, *Halicephalobus*, *Koernia*, *Mesorhabditis*, *Oscheuis*, *Pristionchus*, *Rhabditis*, and *Sclerorhabditis* are phoretic associates with 13 genera of ants [298].

Heterorhabditidae

[2 total associate records | 2 parasite records]

The Heterorhabditidae, along with the Steinernematidae, are entomopathogenic nematodes with interesting bacterial associations [298]. The nematodes infect ants through the transmission of food and, after gaining entrance to the hemocoel, release symbiotic bacteria that kill the ant host. Records of nematodes from this family infecting ants are known only from the laboratory, no natural infections have yet been observed. *Heterorhabditis bacteriophora* has been found in association with *Solenopsis invicta* and *S. richteri* ([303], within [298]).

Steinernematidae

[8 total associate records | 8 parasite records]

The Steinernematidae, along with the Heterorhabditidae, use symbiotic bacteria to kill their ant host after entering the hemocoel following trophallaxis [298]. Though only known from laboratory infections, *Steinerema carpocapsae* has been recorded successfully infecting ants from the genera *Acromyrmex*, *Camponotus*, *Myrmica*, *Pogonomyrmex*, and *Solenopsis* (see review within [298]).

Physalopteridae

[1 total associate record | 1 parasite record]

Skrjabinoptera phrynosoma is the sole species of this family recorded infecting ants. The final hosts of this nematode are lizards, who excrete nematodes containing infective eggs in their feces. Foraging ants feed these nematodes and their eggs to brood, where the nematodes develop from larvae to juvenile stages as the ant develops through eclosion. When lizards eat the infected adult ants, the life cycle is completed. Poinar (2012) notes that infected workers containing more than 10 nematodes were still active, but had enlarged, lighter-colored gasters [298].

Seuratidae

[1 total associate record | 1 parasite record]

Only one record of a nematode from the family Seuratidae, normally known to infect vertebrates, has been found infecting ants. *Rabbiium paradoxus* was found infecting *Camponotus castaneus* in the United States [304]. It is thought that ants became infected after ingesting nematode eggs contained within lizard feces. Poinar (2012) notes that parasitized workers had swollen gasters and were found foraging during the day, which would make them easier targets for predation and thus trophic transmission of the nematode [298].

Tetradonematidae

[3 total associate records | 3 parasite records]

We report 3 records of Tetradonematids infecting ants from two genera: *Tetradonema* and *Myrmeconema*. *Tetradonema solenopsis* has been found parasitizing *Solenopsis*

invicta in Brazil ([305], within [298]); most life cycle details and the impact of infection due to these nematodes remain unknown [298].

Myrmeconema is a very interesting genus consisting of two species (*M. antiqua*-fossil, *M. neotropicum*- extant) that make use of trophic transmission in order to complete their life cycle [298, 306]. Ant pupae are fed female nematodes; once the ant becomes an adult, nematode egg masses are released into the ant's hemocoel and change the color of the ant's gaster from black to red. Infected ants hold their gasters high in the air, which combined with the red coloration of their gasters, makes them appear to be fruit. Birds eat the ants and the nematode finishes its life cycle inside its final host. Though *M. antiqua* is a fossil species and thus its life cycle details cannot be definitively described, it is thought that its life history is very similar to that of *M. neotropicum* [298].

Mermithidae

[17 total associate records | 17 parasite records]

Mermithid nematodes are well-known parasites of ants due to the stunning examples of behavioral manipulation that they cause (reviewed in [307]). While many mermithid species reported from ants are undescribed (see Poinar et al. 2006), we report 8 genera (1 fossil, 7 extant) infecting ants: *Agamomermis*, *Allomermis*, *Camponotimermis*, *Comanimermis*, *Heydenius* (fossil), *Mermis*, *Meximermis*, and *Pheromermis*.

The general life cycle of a mermithid nematode is reviewed in Poinar (2012) [298]. Foraging ants collect protein sources that serve as paratenic hosts for the nematode; these paratenic hosts are fed to ant brood wherein the nematode initiates development. Once the nematode has finished developing inside the now adult ant, it induces its host to seek out water. Once there, the adult nematode escapes its dying ant host to complete the remainder of its life cycle.

2.4.9 Hymenoptera

[442 total association records, 354 parasite records]

Hymenoptera are a large and diverse order of insects containing the ants, bees, wasps, and sawflies. Hymenoptera have a wide range of lifestyles, from solitary to eusocial, and free-living to parasitoid. The parasitoid lifestyle in the Hymenoptera had a single origin early in the Euhymenopteran lineage [308, 309], with ectoparasitoidism

as the ancestral mode. Many independent transitions to endoparasitism have occurred within parasitoid lineages [308,310]. Interestingly, the evolution of complex brain structures known as mushroom bodies was concurrent with the acquisition of parasitoidism and not with the rise of sociality as previously thought [311]. Interested readers should refer to Whitfield (1998) [308], Whitfield (2003) [309], and Eggleton and Belshaw (1993) [312] for reviews of hymenopterans as parasitoids.

Hymenopteran parasitoids of ants have been well-reviewed by Lachaud and Perez-Lachaud (2012) and by Schmid-Hempel (1998) [91, 181]. We summarize interesting aspects of parasite biology for each hymenopteran family below and report 442 records of Hymenoptera from 12 families associated with ants (Table 2.2). The majority of these records come from the Eucharitidae, which are ecto- and endoparasitoids of ant brood, followed by the Diapriidae, Braconidae, and Encyrtidae.

Mutillidae

[5 total association records | 5 parasite records]

The Mutillidae are a large family of wasps commonly known as ‘velvet ants’. Mutillid larvae are idiobiont ectoparasitoids of enclosed host stages (e.g. pupae) [313]. In many cases, direct parasitism of ants by mutillids has not been observed, but the association is inferred (Brothers 1994). Many mutillids are parasitoids of commensals living inside ant nests (e.g. beetles) and are not parasitoids of the ants themselves. In other instances, mutillids are Mullerian mimics of ants [313]. In a recent revision of the mutillid subfamily Rhopalomutillinae, Brothers (2015) noted that the biology of the wasps indicated that they might parasitize ants [314]. More work is needed to determine the extent of host-parasite relationships between the Mutillidae and ants.

While Mutillidae commonly parasitize solitary bees and wasps [313,315], only five species within the genus *Ponerotilla* have been reported (presumably) parasitizing immature workers of the ponerine ant *Brachyponera lutea* in Australia ([316], within [91]. The general life cycle of mutillids parasitizing insects seems to be that following mating, female mutillids independently enter insect nests and deposit eggs near larvae and pupae. Developing wasps then feed and kill their larval/pupal hosts as ectoparasitoids.

Bethylidae (Superfamily Chrysidoidea)

[2 total association records | 2 parasite records]

The Bethyidae are a family of aculeate wasps within the superfamily Chrysidoidea. Most Bethyidae are parasitoids of Coleoptera and Lepidoptera, acting as ectoparasitoids of their larvae [22]. Thus, several bethylids have been associated with ants, probably as ectoparasitoids of commensal beetles or lepidopterans living in their nests ([317], reviewed in [22]).

One bethylid genus, *Pseudisobrachium*, has been implicated as infecting ant brood, though its exact association is unclear ([318,319], within [22,91]). *Pseudisobrachium* is associated with ants in the genera *Aphaenogaster* and *Solenopsis* ([318,319], within [22] 1982).

Chalcididae (Superfamily Chalcidoidea)

[5 total association records | 5 parasite records]

Chalcidid wasps are endoparasitoids (occasionally ectoparasitoids) of Diptera and Lepidoptera, though other orders of insects, including Hymenoptera, may be infected [182]. We report five species of chalcidid wasps from the genus *Smicromorpha* infecting ants, though some of these reports have not been conclusively confirmed (see discussion in [320]). All are parasitoids of the arboreal weaver ant, *Oecophylla smaragdina*, in the Indo-Australia region [181, 182, 320]. Weaver ants use their silk-spinning larvae to create their leaf nests in trees; *Smicromorpha* deposits eggs on the larvae while they are exposed during the nest building process ([321], within [320]). It appears that the association between *Smicromorpha* and *Oecophylla* is unique, and given the overlapping distributions of both these genera in mainland Southeast Asia, reports from that area should be expected as more surveys are conducted [320].

Encyrtidae (Superfamily Chalcidoidea)

[41 total association records | 1 parasite record]

The Encyrtidae are a family of wasps that are endoparasitoids or egg predators primarily of scale insects, but also other orders of insects [182]. Many encyrtid wasps are reported as associates of ants, but few of these are actually parasitic. As reviewed in Perez-Lachaud, Noyes, and Lachaud (2012): “Numerous cases of associations of

encyrtid wasps with ants have already been reported. In the majority of these cases, however, wasps are associated only indirectly with ants (interference associations) through primary parasitism of the trophobionts (Coccoidea), which are exploited and protected by ants. Suspected direct parasitism cases are unusual, and no direct attack of encyrtids on ants has ever been demonstrated” [181].

Only recently has an encyrtid been found as a true primary parasite of ants. A single species, *Blanchardiscus pollux*, is reported infecting the ponerine ant *Neoponera goeldii* in French Guiana (host species is listed as *Pachycondyla goeldii*, [322]). More surveying might reveal additional encyrtid wasps that are primary parasites of ants.

Eucharitidae (Superfamily Chalcidoidea)

[199 total association records | 199 parasite records]

Wasps within the family Eucharitidae are parasitoids of ant brood including larvae, pre-pupae, and pupae [182, 323–326]. Eucharitid wasps colonized the ants approximately 72 million years ago [310] and are known worldwide [324, 327]. Murray et al. (2013) provide a wonderful study on the phylogeny of Eucharitidae as it relates to that of their ant hosts: “Eucharitidae exhibit a general trend of ant subfamily colonization (host-switching) occurring infrequently at an early time period, followed by high host conservatism (phylogenetic affinity) at the ant-subfamily level in extant lineages” [310].

We report 109 species in 29 genera as parasitoids of 30 genera of ants. Many additional eucharitid species have been described, but full life history details including their associated host ant species remain unknown (see [327, 328]). It can be expected that as these life history details are filled in, numerous host records will be added to the database.

The general life cycle of eucharitid wasps can be described as follows: adult female eucharitid wasps locate the microhabitat of potential hosts and lay eggs on nearby vegetation, which can include leaves and fruit [327]. These eggs develop into first-instar planidial larvae (described by [329, 330]), which must then make contact with the ant host [181, 324]. It is currently unknown whether the larvae actively seek out potential hosts, or are picked up through passive contact with foraging ants [182]. Inside the nest, the planidial larvae need to gain access to the brood, which is accomplished through phoretic transfer from workers tending the brood.

Once they have accessed ant larvae, eucharitid wasps can either be internal or external parasitoids of their ant host [182], both of which ultimately result in host death. It appears that external parasitism (ectoparasitism) is the most likely ancestral state, with internal parasitism (endoparasitism) having evolved independently in at least three lineages of the Eucharitidae [331]. As either ecto- or endoparasites, eucharitid larvae generally wait until the host has reached the pre-pupal stage before continuing their larval development and can pupate inside the host cocoon or naked inside the nest [182]. Upon completion of their development, adult eucharitid wasps must successfully exit the ant nest in order to find mates. It seems that some eucharitids might exploit the hygienic behavior of their hosts, using imperfectly mimicked host cuticular carbon profiles in order to be identified as intruders and personally escorted out [332]. How far the adult wasps disperse is not well known, but Ayre (1962) found that mating between *Pseudometagea schwarzii* wasps occurred almost immediately following emergence, and they laid their eggs within the foraging area of their host ant nest [333].

Despite their worldwide distribution and parasitoidism of many ant genera, eucharitid wasps do not seem to impose a major cost on ant colonies. Ayre (1962) writes: “Though parasitism is very high within the centers of infestation, the influence of *P. schwarzii* on the population size of *L. neoniger* is doubtful, even within these centers.” [333]. This observation has been made by others; Lachaud and Perez-Lachaud note, “Nevertheless, considering the extremely high nest densities recorded in the study zone [334], the *E. ruidum* population did not appear to be seriously affected by such a high level of parasitism.” [181].

Eulophidae (Superfamily Chalcidoidea)

[37 total association records | 12 parasite records]

The Eulophidae are a speciose and globally distributed family of wasps that are primarily parasitoids of concealed larvae [182]. Eulophid wasps can be ecto- or endoparasitoids, solitary or gregarious, idiobionts or koinobionts of a diverse array of insects [182].

We report 37 records of eulophid wasps associated with ants. Many of these are nest associates, attacking commensals that live inside ant nests. Of these 37 records, 13 are instances where the eulophid wasp is a primary parasitoid of ant brood. These

ant-parasitic Eulophidae comprise the genera *Melittobia*, *Horismenus*, *Myrmokata*, and *Pediobius* infecting the ant genera *Acantholepis*, *Camponotus*, *Crematogaster*, and *Formica*.

Eupelmidae

[2 total association records | 2 parasite records]

The Eupelmidae are a family of wasps that are parasitic on the immature stages of other insects [182]. Only two species of Eupelmidae are brood parasitoids of ants, both within the genus *Anastatus*. *Anastatus myrmecobius* parasitizes *Temnothorax purpurata*, and *Anastatus redivii* parasitizes *Pseudomyrmex elongata* [182].

Eurytomidae (Superfamily Chalcidoidea)

[12 total association records | 10 parasite records]

The Eurytomidae are a family of wasps with a diverse array of biologies associated with plants, ranging from phytophages to parasitoids of phytophagous insects [182]. We report 12 records of eurytomid wasps associated with ants. Of these, 3 species of eurytomid wasps within the genus *Aximopsis* are parasitoids of ants. *Aximopsis affinis* and *Aximopsis aztecicida* parasitize species of *Azteca*, while *Aximopsis sp.* parasitizes *Azteca* as well as a single species of *Camponotus*. Additionally, *Camponotophilus* and *Sycophila* are genera of eurytomid wasps that are non-parasitically associated with the ants *Camponotus sp.* and *Formica obscuripes*, respectively.

Pteromalidae (Superfamily Chalcidoidea)

[2 total association records | 2 parasite records]

Only 2 records of Pteromalidae infecting ants have thus far been recorded. *Pheidoloxenus wheeleri* infecting *Pheidole instabilis* and *Pheidole ceres* in the United States and Mexico are the only records to date ([335], within [91]). Mann (1914) writes that W.M. Wheeler, who first discovered the pteromalid infecting ants, considers the pteromalids to be endoparasites of adults or brood [335]. The rest of the parasite's biology is unknown.

Braconidae (Superfamily Ichneumonidae)

[48 total association records | 47 parasite records]

The Braconidae is a very large family of parasitoid wasps, the second most speciose family within the Hymenoptera [336]. Despite this, only four genera are known to infect ants. We report 50 records of braconid wasps in the genera *Elasmosoma*, *Elasmosomites* (fossil species), *Kollasmosoma*, and *Neoneurus* as known parasites of ants. An additional genus, *Paralypsis*, is reported as an ant associate. Braconidae infect the Formicinae genera *Formica*, *Camponotus*, *Lasius*, *Polyergus*, *Cataglyphis*, and the Myrmicine genus *Messor*.

Braconids oviposit directly into adult ants while they are foraging outside of the nest [337–343], which is unusual amongst hymenopteran parasitoids [344]. Their larvae develop as endoparasitoids that ultimately kill the ant host [22, 345–347]. Fossil evidence of a braconid wasp infecting an ant indicates that parasitism by braconids could date back at least 40 million years [348].

Ichneumonidae (Superfamily Ichneumonoidea)

[35 total association records | 33 parasite records]

The Ichneumonidae is a very large family of parasitic wasps that commonly parasitize the brood of other insects [349]. We report three genera of ichneumonid wasps, *Eurypterna*, *Ghilaromma*, and *Hybrizon* parasitizing ants in the genera *Formica*, *Lasius*, *Myrmica*, and *Tapinoma*. One additional ichneumonid genus, *Pesomachus*, is reported as an associate of ant nests.

While the life history details and host records for many ichneumonid wasps remain unclear, it appears that the ant-parasitic Ichneumonidae oviposit directly into ant brood as they are being carried between nests by workers [343, 350] or in disturbed nests [351]. Following oviposition, the wasps develop as endoparasitoids, ultimately killing their ant hosts [352].

Komatsu and Kinishi (2010) report an undescribed ichneumonid wasp that took much longer to oviposit in its slower-moving *Myrmica kotokui* host than it took other observed ichneumonids to oviposit in their hosts [350]. They suspect that there might be a diversification in the behavioral ecology of the ichneumonid wasps that reflects how quick-moving their host species are.

Diapriidae (Superorder Diaproidea)

[54 total association records | 38 parasite records]

The Diapriidae are a family of small parasitic wasps with a worldwide distribution [353]. While most Diapriidae attack the larval stages of flies, some are endoparasitoids of ant brood or nest associates living within ant colonies (reviewed in [181, 354–357]). The life history details for many species are unknown and how they interact behaviorally with their ant hosts is also largely unknown for the majority of species [358].

Though we have compiled 54 records, there are many undescribed species within genera known to parasitize ants [356], and thus many new records can be expected as the biology and diversity of this family is uncovered. We report 17 genera of diapriid wasps associated with 10 ant genera.

Based on the general biology of the diapriids, it appears that adults likely enter the nest independently and have evolved a suite of morphological and behavioral adaptations to facilitate acceptance [181, 357]. It has been suggested that diapriids originally parasitized Diptera, and over the course of their evolutionary history slowly changed hosts to members of the Formicidae, particularly in the case of the army ant subfamily Ecitoninae, where many dipterans live amongst ant refuse piles ([359], within [357]). Thus we might expect a spectrum of associations, with some diapriids as nest associates of ants and others having evolved to full endoparasitoidism of ant brood. For many of the Diapriidae associated with ants, the true host-parasite relationship is unknown.

For those diapriids that are true parasitoids of ants, it seems likely that the adult wasps do not live inside the ant nests [121]. Fernandez-Marin et al. (2006) note that following emergence from their cocoons, diapriid wasps are very aggressively bitten by the ants: “The primary defense against parasitoid wasps presumably is a behavioral response involving biting or killing adult wasps when they emerge or attempt to invade the nest. In turn, we infer that the wasps’ primary defense is to avoid ants and, secondarily, remain immobile when attacked. The wasps quickly leave the emergence area, which supports our inference, because it reduces the probability that ants encounter them” [121]. Based on colony prevalence rates found in the field, it seems that diapriid parasitism might have a more profound impact on colony demography than that of other parasitoid families (e.g. Eucharitidae, Phoridae) [121,

181], though this hypothesis has not yet been formally examined either empirically or theoretically.

2.4.10 Diptera

[812 total association records | 492 parasite records]

The diptera, or true flies, are a megadiverse insect order estimated to contain 1,000,000 species [360]. Of these, an estimated 16,000 species of dipterans in 21 families are parasitoids [312, 361]. Parasitoidism as a life cycle evolved over 100 times in the Diptera, from ancestors that were mostly saprophagous [312, 361]. Interested readers should refer to both Feener and Brown (1997) and Eggleton and Belshaw (1992) where the ecology, biogeography, and evolution of diptera as parasitoids have been extensively reviewed [312, 361].

We report 812 records of Diptera from six families, the Chloropidae, Ephydriidae, Phoridae, Tachinidae, Helosciomyzidae and Syrphidae as associates of ants. The Phoridae are parasitoids of adult ants and very occasionally ant brood and comprise the vast majority of these associations. The Tachinidae and Helosciomyzidae are parasites and parasitoids of other insects, but few records have been found of them infecting ants. The Syrphidae have long been known as predators living inside ant nests, and only recently have they been recorded as true primary parasites of ants.

Chloropidae

[1 total association record | 1 parasite record]

One record of a fly from the family Chloropidae is known to infect ants. *Pseudogaurax paratolmos* is reported infecting *Apterostigma dentigerum*. Gonzalez et al. (2016) report that *Pseudogaurax* are solitary ectoparasites of ant larvae. They note that parasitized brood were treated the same as non-infected nest mates [362].

Ephydriidae

[2 total association records | 2 parasite records]

We report 2 records of parasitic flies from the family Ephydriidae reported in association with ants. *Rhynchopsilopa* are ectoparasites infecting *Crematogaster* sp. The flies mount and feed on the ants and are not known to cause host mortality [363].

Phoridae

[700 total association records | 485 parasite records]

The Phoridae are a large family comprising many different life history strategies. Parasitoids within the Phoridae parasitize adult ant workers, and rarely, female reproductives or brood [179, 361, 364, 365]. Many additional phorid species have been found in association with ant colonies, as scavengers of nest detritus, as predators of ant brood and injured workers [366], or as other nest associates [367]. While a large number of phorid parasitoids of ants have been described, host records for many species remain unknown or unpublished [368], and associations between some phorid flies and ant hosts remain unclear, so we can expect many more records to be added to this database in coming years. We report 485 parasite records within the Phoridae, comprising 32 genera and 262 species parasitizing 40 unique ant genera and 182 unique ant species. Most of these are primary parasitoids of adult ants, but phorids from 4 genera (*Aenigmatias*, *Apodicrania*, *Nothomicrodon*, and *Pseudogaurax*) are ecto- and endoparasitoids of ant brood.

For the phorids that are parasitoids of adult ants, the general life cycle is as follows. Adult female phorids use visual and olfactory cues to locate and oviposit onto adult ant workers, using recruitment trail pheromones or nest sites of hosts as possible orientation cues [341, 361, 369]. Phorids might capitalize by ovipositing into ants injured during army ant raids [361]. Oviposition can occur in the head, thorax, or gaster of the ant hosts, after which point larval development begins [179]. Larvae feed on the host hemolymph, and in many species, larvae migrate to the host's head, ultimately causing decapitation. The location of this decapitation and the emergence of the adult fly can happen inside the nest, but then exiting the nest before being detected and killed by ant hosts presents a challenge. It appears that some phorid flies might be able to control the behavior of their host, inducing them to leave the colony several hours prior to emergence [370]. The degree to which ant behavior might be manipulated by phorid parasitoids and the mechanisms underlying such manipulation are unknown.

Many phorids associated with ants are not parasitoids and it seems that parasitoidism evolved following a scavenger-host association [361]. Thus, we find a diverse array of associations between phorids and ants, many of which have not been fully elucidated.

Phorids have been investigated extensively for their potential use as biological control agents against pestiferous ant species (reviewed in [371–373]). The impacts of phorid parasitoids on colony functioning appears to be low; as noted in Morrison (2012):

‘*Pseudacteon* phorids attack host workers involved in foraging, interspecific interactions, and colony defense - all relatively dangerous activities. Thus most of the workers parasitized are engaged in high-risk activities and near the end of their natural lives, and colony fitness is affected to a lesser degree than if workers were parasitized at random with respect to age.’

[372]. Porter et al. (1995) also find that the impact of phorid parasitism on colony mortality is low, but indirect effects of phorid parasitoidism might serve to mediate interspecific competition:

‘Based upon our observations in the field [374], and those of other researchers [375], we do not expect that species of *Pseudacteon* would act as direct biological control agents in the classical sense of reducing the number of ants or of inducing colony mortality. Rather, when phorids are present, ant activity declines favoring other potential competing species. Thus, we predict that the effect of phorids would be to change competitive hierarchies, and not greatly increase worker mortality.’

[376]. In reviewing the phorid parasitoids of leaf-cutter ants, Folgarait (2013) notes that the overall parasitism rate is higher than that of *Pseudacteon* parasitizing *Solenopsis*, and that prevalence likely depends on the health status of the colony [373].

Tachinidae

[16 total association records | 2 parasite records]

The Tachinidae are a large family of true flies that are parasites or parasitoids of other arthropods. Few records of association between tachinids and ants exist; we report 16 associations, in which only 2 have been reported as parasitic. *Strongylogaster globula* is an endoparasite of *Lasius* queens [377], but this has not been observed again. Rettenmeyer et al. (2011) report several tachinid species within the genus *Calodexia* associated with *Eciton burchelli* during swarm raids, but the nature of the relationship between the tachnids and the ants is unknown [378].

Helosciomyzidae

[1 total association record | 1 parasite record]

We report only 1 record of flies from the family Helosciomyzidae parasitizing ants. *Helosciomyza subalpine* is a brood ectoparasite of *Monomorium antarcticum* (listed as *Chelaner antarcticus*, [379]) in New Zealand. The fly larvae chew holes in the integument of the ant larvae, and feed on the liquid exudate until the ant larvae dies a few days later.

Syrphidae

[92 total association records | 1 parasite record]

Syrphidae are a family of flies in which the adults commonly feed on plant material (nectar, pollen), while the larvae are insectivorous or saprotrophic. The known biology of the Syrphidae associated with ants is well-reviewed in Reemer (2013) [380] and Perez-Lachaud et al. (2014) [381]. While the syrphid subfamily Microdontinae have long been associated as myrmecophiles living in ant nests as predators of ant brood (reviewed in Reemer 2013), the first truly parasitic syrphid fly was only discovered in 2014. We report 92 records of Syrphidae associated with ants, of which 1 record involves a true case of parasitism.

Perez-Lachaud et al. (2014) report the first record of a syrphid as a primary parasite of ants, *Hypselosyrphus trigonus* infecting brood of *Neoponera villosa* (reported as *Pachycondyla villosa*) in Mexico [381]. Unlike the predatory Microdontinae which lay eggs in the vicinity of the ant nest [361], it appears adult *H. trigonus* females oviposit eggs directly on the ant brood. As noted by Perez-Lachaud et al. (2014), *N. villosa* have not been observed moving their nests, thus it seems likely that the syrphid flies must enter the ant nests independently to access and oviposit onto brood [381].

Syrphids within the family Microdontinae are specialized predators of ant brood. Adult Microdontinae lay their eggs outside of ant nests, and these larvae enter and develop inside ant nests. The ability to live undetected inside ant colonies is no simple feat; syrphids in the genus *Microdon* are able to mimic the cuticular hydrocarbons of their ant hosts to avoid detection [382, 383]. Possessing the ability to mimic one's host likely necessitates host specialization for these Microdontinae [380].

The impact of both predatory and parasitic syrphids on host ant colony functioning is unknown, but potentially large (reviewed in [380]).

2.4.11 Strepsiptera

[23 total association records | 23 parasite records]

The Strepsiptera ('twisted wing parasites') are a small order of insects that spend much of their lives as entomophagous parasitoids of other insects [384, 385]. Females in all strepsipteran families other than the Mengenellidae spend their entire lives inside their hosts, while adult males are free-living but extremely short-lived. Only strepsipterans in the family Myrmecolacidae parasitize ants.

Life cycle of strepsipterans in the Myrmecolacidae

Female strepsipterans reproduce viviparously; the first larval instars consume their mother from the inside and then emerge. Following emergence, these free-living larvae then actively seek out hosts. In the case of the Myrmecolacidae, males and females exhibit sexual dimorphism in their host choice, with males parasitizing ants while females parasitize insects from other orders. Having found an ant host, the male strepsipteran larvae penetrate the cuticle and once inside, go through several larval stages before pupating. This development itself does not kill the host, rather, the host must remain alive until after the strepsipterans have completed their development. When the males are ready to emerge, they leave the host via the puparium, leaving a hole in the host that often becomes colonized by fungi [385].

Ants parasitized by strepsipterans have been observed behaving unusually, as summarized by Kathirathamby et al. 2010:

'It is hypothesized that stylopized ants do not abandon and wander away from the nest [180, 386]. However, just before the emergence of the free-living male strepsipteran from the partially endoparasitic puparium, the ant leaves the nest, and it is its behaviour during this period that was observed by Ogloblin (1939). Ogloblin stated that, "when ants are stylopized, they change their nocturnal habits, acquire positive phototropism, and lose their social instincts, abandoning their nests and rambling singly, often climbing high on grass and bush [387]".'

[388].

Host associations

The very short lifespan of the free-living, adult male strepsipterans and the entirely endoparasitic lifestyles of adult female strepsipterans make recording host associations with these insects difficult. Though ants were first recorded being infected by strepsipterans by Westwood in 1861, our knowledge of host records remains limited, perhaps due in part to the ant collecting methods often employed by myrmecologists [389].

Known host associations between strepsiptera and ants are summarized in [388–390], and the Strepsiptera database [183]. Many additional strepsipterans in genera known to infect ants have been described, but have unknown host associations (see Strepsiptera database). We report 23 records of strepsiptera from the genera *Caenocholax*, *Myrmecolax*, and *Stichotrema* infecting ants from 9 genera.

Myrmecolacidae

[23 total association records | 23 parasite records]

The Myrmecolacidae are the only family within the Strepsiptera to use ants as hosts during their life cycle. Currently, three genera within the Myrmecolacidae are known: *Caenocholax*, *Myrmecolax*, and *Stichotrema*.

Caenocholax fenyesei (11 records) is a species complex with cryptic diversity (Hayward et al 2011); our records database will grow as this diversity is unraveled and further host associations are uncovered. *Caenocholax fenyesei* sensu lato has been recorded parasitizing *Camponotus*, *Crematogaster*, *Dolichoderus*, *Myrmelachista*, *Pheidole*, and *Solenopsis* in North and South America.

Myrmecolax (6 records) has been recorded parasitizing *Camponotus*, *Eciton*, and *Pachycondyla* in the Neotropics and Indo-Australia region.

Stichotrema (6 records) has been recorded from *Camponotus*, *Crematogaster*, *Pheidole*, *Pseudomyrmex*, and *Solenopsis* in South America, Africa, and Southeast Asia.

2.5 Results: Host-specific

In the previous sections, we provided parasite-specific details on major trends in life history and epidemiological traits across parasite families. In this section, we take an

ant-centric view and look at how known parasite records assort across ant subfamilies and genera.

Parasite records across ant subfamilies

Of the 17 currently recognized and extant ant subfamilies [7], only 10 (58.8%) have any reported associate, parasite, or parasitoid records (Fig. 2.12). The subfamilies Myrmicinae and Formicinae had the highest number of total associate records, with 743 and 647 records, respectively. These were followed by the Ponerinae (168 records) and Dorylinae (158 records).

Parasite records across ant genera

Only 81 of the 333 (24.3%) currently recognized extant ant genera [7] have parasites or parasitoids reported infecting them (Table 2.4, Figure 2.13); 87/333 genera (26.1%) have associates of any relationship reported with them. Most of the ant genera reported with parasites records had fewer than five records associated with them (median number of records = 5, Figure 2.14). The ten ant genera with the most parasite records were *Camponotus* (192), *Solenopsis* (144), *Formica* (132), *Pheidole* (85), *Polyrhachis* (69), *Lasius* (67), *Atta* (61), *Pachycondyla* (60), *Acromyrmex* (59), and *Odontomachus* (32).

Potential records bias

Bias is most certainly present in the records of parasites and parasitoids infecting ants that we have collected here. This bias is due to the preferential study of certain ant genera over others as well as the preferential study of certain parasite genera over others (see discussion).

To begin to assess where bias might be present in the reported parasite records, we plot the number of parasite records reported for a given ant genus as a function of the total number of recognized, extant species in that genus (Figure 2.15). There is a weak linear correlation between the number of record parasite associations and the number extant species in an ant genus (linear regression, adj. $R^2 = 0.38$), suggesting that while the diversity of species within a genus is probably important, other factors might also be contributing to the patterns in parasite records that we observe. For example,

Strumigenys is a very large genus, consisting of 837 extant species, but we only report 1 parasite record associated with that genus. In contrast, *Solenopsis* is a medium-sized genus with 195 species, for which we report 144 parasite records. While both *Strumigenys* and *Solenopsis* are small, subterranean-dwelling ant genera, *Solenopsis* is an invasive, pestiferous genus and researchers have been actively surveying for potential biocontrol agents to use against them. Thus, this likely accounts for the large number of parasite records reported with *Solenopsis*.

2.6 Discussion

The major goal of this work was to collect as many extant records of parasitic organisms infecting ants as we could, and from these records, synthesize major patterns in the natural history and epidemiological relationships of these parasites with their ant hosts. To that end, we report 1,415 records of parasites and parasitoids in 51 families infecting 81 genera of ants (Appendix A Table A.1, Table 2.5).

The majority of the parasitic organisms we report infecting ants are parasitoids (89.5%, 167/1,415 records, Figure 2.6), which require death of the ant host as a developmental necessity. Most parasitic organisms infecting ants encounter the hosts that they will subsequently infect in the extranidal (outside of the nest) environment (primary encounter- 68.6%, 970/1,415 records, Fig. 2.7), though others are able to enter colonies independently of host behavior (independent encounter - 10.2%, 144/1,415 records, Fig. 2.7). To complete their life cycles, most parasitic organisms infecting ants only need to use a single host (direct transmission- 89.1%, 1,261/1,415 records, Fig. 2.8), though the use of indirect life cycles involving multiple hosts predominates amongst worms (Trematodes, Cestoda, and Nematoda, Fig. 2.8). Finally, most parasitic organisms infecting ants need to leave the nest to complete their life cycles before they are capable of transmitting to new ant hosts (*ex-nido* transmission- 88.3%, 1249/1,415 records, Fig. 2.9).

Of the major taxonomic groups infecting ants, Order Diptera (flies), Phylum Fungi, and Order Hymenoptera (parasitic wasps) predominate, accounting for 34.8%, 25.6%, and 25.0% of the records, respectively (Fig. 2.5). Viruses and bacteria account for only 1.1% of the total parasite records (16/1,415 records, Fig. 2.5). Some parasite groups are likely undersampled, in most cases due to lack of targeted surveys and particularly for those parasites that are difficult to identify (e.g. Strepsiptera).

Only 10 out of the 17 extant ant sub-families have records of parasitic organisms associated with them (Fig. 2.12). Surprisingly, less than 25% of all currently recognized ant genera have any parasite records associated with them (81/333 ant genera, Fig. 2.13). Of the few genera that do have parasite records, the median number of records is 5 (Fig. 2.14), with the genera *Camponotus*, *Solenopsis*, *Formica*, *Pheidole*, and *Polyrhachis* comprising the majority of hosts with reported parasites (192, 144, 132, 85, and 69 records, respectively). The number of reported parasite records for a genus has a general positive correlation with the number of ant species in that genus, but the fit of a simple linear regression to the data is poor (Fig. 2.15), suggesting that many ant genera may be undersampled. Other ant genera, particularly those with invasive or pestiferous species, may have received more scrutiny in the quest to identify possible bio-control agents, leading to a preponderance of records for those genera.

2.6.1 Why does parasitoidism predominate?

The predominance of parasitoidism (89.5%) amongst the reported records may seem counterintuitive at first glance - killing off hosts as developmental necessity leaves fewer future hosts to infect. However, ants are eusocial organisms and their fitness lies at the level of the colony, not at the level of the individual [38, 391]. Thus, killing off one individual, or even many individuals, may have negligible impacts on lifetime colony fitness. Indeed, the flexible division of labor that is the hallmark of ant colonies [5, 49, 61] likely allows colonies to buffer the loss of individuals whether it is due to disease, predation, or inter- and intra-specific competition. Furthermore, the presence of age-related polyethism in many ant species [5] means that many of the individuals infected and killed by parasites (particularly those which use primary encounter strategies) are amongst the oldest in the colony and are thus expected losses. In this light, parasitoids may simply be imposing an extra mortality term on these oldest age classes. Provided that this extra mortality term doesn't over-run what the colony can replace, the parasitoids benefit and colonies can buffer the loss.

While this answers why parasitoidism could be a viable strategy, it doesn't answer why parasitism does not dominate the reported records. Parasitism as a strategy doesn't require the death of the host as developmental necessity, but in ant hosts, death can nevertheless occur. Furthermore, in the records we report, parasitism tends to co-associate with *in-nido* transmission strategies (Fig. 2.11), in which direct ant-

to-ant transmission can occur inside the nest. Coupled with the high-density living conditions of many ant species (reviewed in [89]), epidemics within the colony could thus occur. Such parasites, such as viruses, bacteria, and generalist fungi, have likely imposed a strong selective force on ancestral ants prior to their transition to eusocial living, necessitating the innovation of the suite of immunological, behavioral, and organizational defenses that we find in extant ant societies (reviewed in [91,97,97,129]). Parasites with epidemic potential inside colonies may have been actively selected against by these strong anti-parasite defenses, may make use of a broad host range to account for colony burnout, or may have evolved reduced virulence inside ant colonies over time. These parasites may also be lacking in reported records because they are taxonomically harder to culture and/or identify, and ants killed by viruses or bacteria may simply be harder to find in field settings.

2.6.2 Why do most parasitic organisms of ants use *ex-nido* transmission?

Ex-nido transmission, in which parasitic organisms must leave the ant colony to complete development, find other hosts, or mate, is extremely common across the majority of taxa infecting ants. *Ex-nido* transmission predominates amongst the worms and insects, and it is also common among specialist fungal parasitoids (e.g. *Ophiocordyceps*). For parasites that use multi-host life cycles (e.g. worms), *ex-nido* transmission is a natural consequence of needing to find hosts that do not live inside ant colonies. For others, their development requires specialized microclimates that cannot be found inside nests (e.g. ‘zombie-ant’ fungi, *Ophiocordyceps*, [171]). But for many parasites that use direct life cycles only requiring ant hosts, why bother leaving the bountiful and protected confines of the colony?

Organisms are generally quite good at recognizing self from non-self, and the ant colony superorganism is no exception. Ants live in a chemical world ([5] p.197 - 297), and are constantly assessing nest mates for their signature colony smell via hydrocarbons that are applied across the ant’s cuticle. Ants can quickly discriminate nest mates from non-nest mates, and experiments have shown that nest mates that have been covered in the hydrocarbons of other colonies are shown aggression [392, 393]. Accordingly, ant colonies are typically on high alert for any potential intruders. For parasitic organisms that utilize free-living stages in their life cycle (e.g. adult

flies, worms), rapid detection once they are outside of their ant host is likely. Thus, it becomes imperative for these organisms to get outside of the colony quickly. For parasitic organisms that do use *in-nido* transmission, the strong recognition systems of colonies can act as a further barrier to within-nest disease transmission. Infected individuals can be recognized and removed from colonies [60, 146]. The adoption of *ex-nido* transmission strategies is therefore either a biological necessity on the part of the parasite, or likely a consequence of strong anti-intruder defenses by ant colonies.

For some parasites that require extended periods of development inside their ant host, avoiding detection as ‘non-self’ is critical. These parasites need their infected ant hosts to remain inside the nest and continue receiving food and to that end, may have evolved the ability to mask their own smell whilst inside their hosts. For example, it has recently been shown that ants infected by the ‘zombie ant’ fungi *Ophiocordyceps*, which can take weeks to grow before it kills its host, are not discriminated against by their non-infected nest mates [394], even though they are filled with fungi as they near death [241, 257]. Social parasites and associates that live extended lives inside ant nests also need to avoid host detection (reviewed in [395]). Other parasitic organisms may exploit the sophistication of the colony recognition system for their own aims by manipulating the cuticular hydrocarbons of their infected hosts over time. For example, nematodes infecting ants require a long period of development inside their ant host; however, they also need to access other host species in aquatic environments. To this end, they may abruptly change the cuticular hydrocarbon profile of their infected host so that nest mates treat the ant aggressively, forcing it out of the colony (E. Sola Gracia, personal communication), and getting it one step closer to where its next transmission event will occur.

2.6.3 Patterns in the records of parasitic organisms infecting ant genera

The observed patterns in parasitic organisms infecting ants are the result of three major factors, discussed below: (i) ant and parasite ecologies, (ii) ant and parasite evolutionary and co-evolutionary histories, and (iii) biases in how records have been collected.

i. Ant and parasite ecologies

The association of ants and parasites depends on both their evolutionary past (below) as well as their ecological present. Certain ant nesting or foraging ecologies may pre-dispose them to associations with certain parasites or parasitoids. For example, nesting on or in soil or leaf litter may pre-dispose ant species to infections by generalist fungi, whereas we may expect to find fewer records of generalist fungi infecting arboreal species. We may expect to find more infections of brood in ant species that are nomadic or polydomous, as in these situations brood are moved around and might be more exposed to parasitic organisms that infect using primary encounters. For ant species that tend hemipterans for their honeydew, we might expect to find instances where viruses or bacteria known to infect hemipterans have made host jumps into ants. Indeed some ant colonies nesting near bees have been found harboring viruses that typically infect bees [203]. Machine learning techniques (e.g. boosted regression trees, [396]) have been used to correlate host life history traits with parasite records for other animal groups [81]. Future work could apply this methodology to understand which ant traits correlate to observed parasite records, and to predict parasite-host combinations for which we have not yet found association records.

ii. Ant and parasite evolutionary histories

The evolutionary pasts of both ants and their parasites have played a role in determining their extant relationships reported here. Though a comprehensive treatment of how parasite records assort across the ant phylogeny is outside the scope of this current work, it could be helpful to lay the future groundwork for this using some general concepts borrowed from the theory of island biogeography [397, 398]. Ant sub-families and genera can be imagined as host islands colonized by parasites. As the ants diversified, these host islands may have shrunk (e.g. become more specialized in their ecological niche, changed habitats or geographic range), presenting a challenge to their parasites. Not all of the parasites may have made the transition alongside their host and for those that did, host ecological specialization may have fostered subsequent parasite specialization or diversification. Additionally, throughout the host diversification process, new parasite families, genera, and species were arising or coming into contact with these ant host islands, providing opportunities for new colonization events.

While it will be difficult to tease apart the full evolutionary history of ants and their parasites, the rich phylogeny of the ants [4, 30] coupled with that of some of their parasites (e.g. eucharitid wasps, Murray and Heraty 2013), will make uncovering parts of this story possible. For example, Murray and Heraty (2013) found that eucharitid wasps, which exclusively parasitize ants, made hosts shifts early in their evolutionary history, but then maintained host conservatism even after dispersal events and speciation [310]. Additionally they found congruence in the phylogenies of ants and eucharitids, suggesting that their evolutionary histories are more similar than random chance alone would predict. Hopefully, as more associations between ants and their parasites become known and as phylogenies become better resolved, we can start piecing together the larger evolutionary story of ants and their parasites.

iii. Biases in parasite records

There is no doubt that bias exists in the parasite records that we report here. Bias exists in which parasitic organisms have been the most extensively studied, and indeed, our knowledge of many particular parasite groups is due to one or several individuals who have championed those taxa and made studying them their life's work. There remain many additional parasite taxa infecting ants that are in dire need of natural historians to take up their cause. Our understanding of the relationships between ants and their parasites has also been hindered by observational bias; it is much easier to notice larger parasites, such as worms and insects, than microscopic parasites (e.g. viruses, bacteria) that have only recently become culturable or identifiable due to methodological advances. One case in point is that of viruses- the first virus known to infect ants was first identified in 2004, though ants are likely host to many viruses [193]. As we begin surveying for parasites and parasitoids more explicitly, more records of ant-parasite association will undoubtedly be discovered.

Bias is also present in the ant genera that have been most studied. Certain ant genera have ecologies that make them more amenable to study. For example, even though the genus *Strumigenys* is quite speciose (837 species), their small size and cryptic nesting ecologies make them more difficult to study generally, and thus we know far less about their general biology and their interactions with parasites. In contrast, other ant genera are infamous for their roles as invasive or pestiferous species (e.g. fire ants, leaf cutter ants, crazy ants, argentine ants) and they have been actively

surveyed for natural enemies that could help control their populations. Accordingly, for these genera, we have far more reported parasite records.

2.6.4 Open questions, future directions, and a call to action

In this work, we have assembled known records and synthesized major patterns in the life history traits of parasites infecting ants. This provides a first step towards approaching the many outstanding questions and open areas of research that remain, some of which we detail here. Firstly, we still lack knowledge of how individual loss due to disease impacts colony level survival and fitness, or how this impacts colonies at different stages of development (i.e. incipient or mature colonies). We don't know how intensely colonies experience parasite pressure, whether certain parasites predominate in exerting that pressure, and how that parasite pressure scales with latitude or other biogeographic factors. We have limited understanding of inter-colony and metapopulation parasite transmission dynamics. We also have little understanding of how parasites of ants impact the larger communities in which they reside. In answering these questions, we will be positioned to better understand how sociality impacts parasite diversity, how parasite diversity impacts the evolution of sociality, and how parasite virulence evolves with social hosts.

We hope that this work serves as a call to action, to myrmecologists, to parasitologists, and to evolutionary ecologists. In order to understand the ecological success of the ants, we need to understand the relationships that they have had with their parasites, both now and over evolutionary time. To further appreciate parasite diversity and understand the roles of parasites in ecological communities, we need to understand the relationships that they have with their hosts. Finally, the ants, with their well-resolved phylogeny and diversity of host ecological traits, offer an exciting opportunity for testing theories of evolutionary ecology, and present a comparative foil to other social living groups.

Acknowledgments

We gratefully acknowledge the many natural historians who have collected records of parasites infecting ants and other social insects. Their hard, often underappreciated, work provides the foundation upon which all of our biological knowledge is built. We

would like to thank Jessica M. Conway for comments and helpful feedback on earlier versions of this work.

2.7 Figures and Tables

Figure 2.1: Schema of parasite encounter modes.

Parasite encounter mode

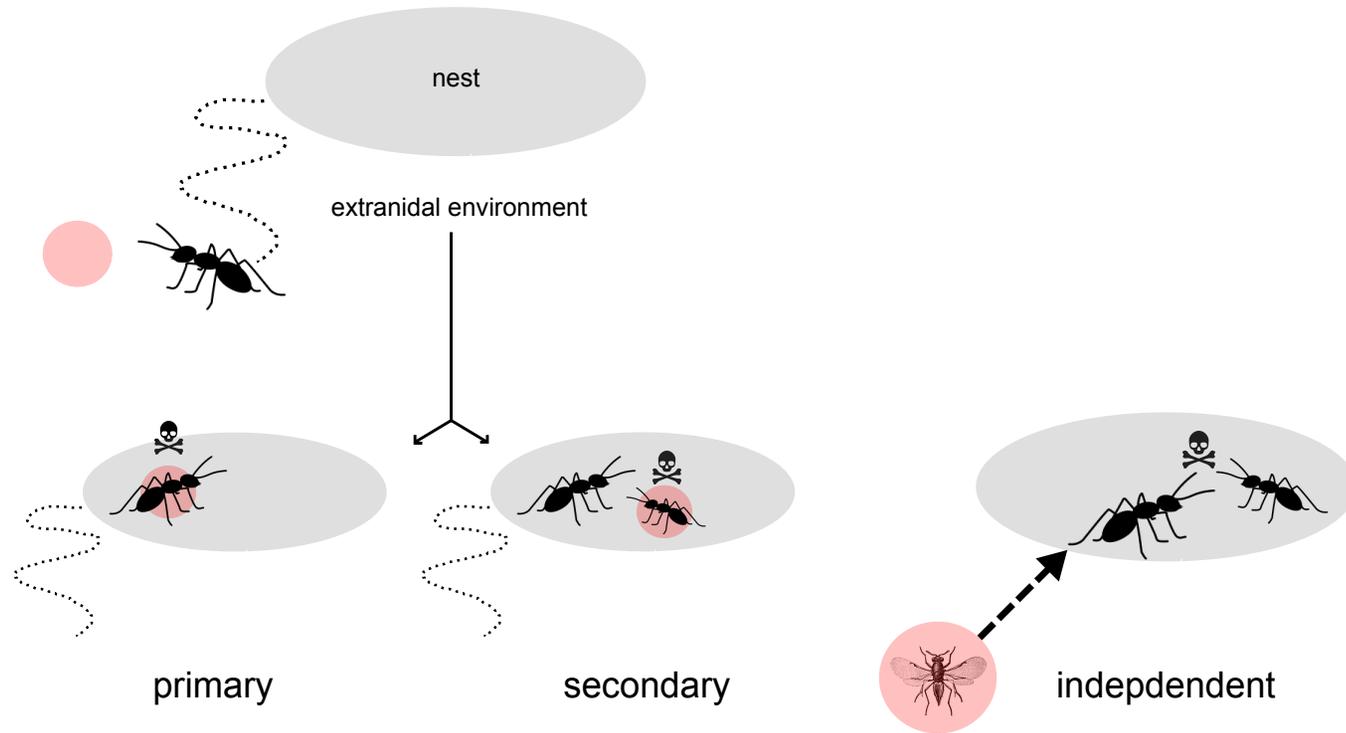


Figure 2.2: Schema of parasite transmission modes.

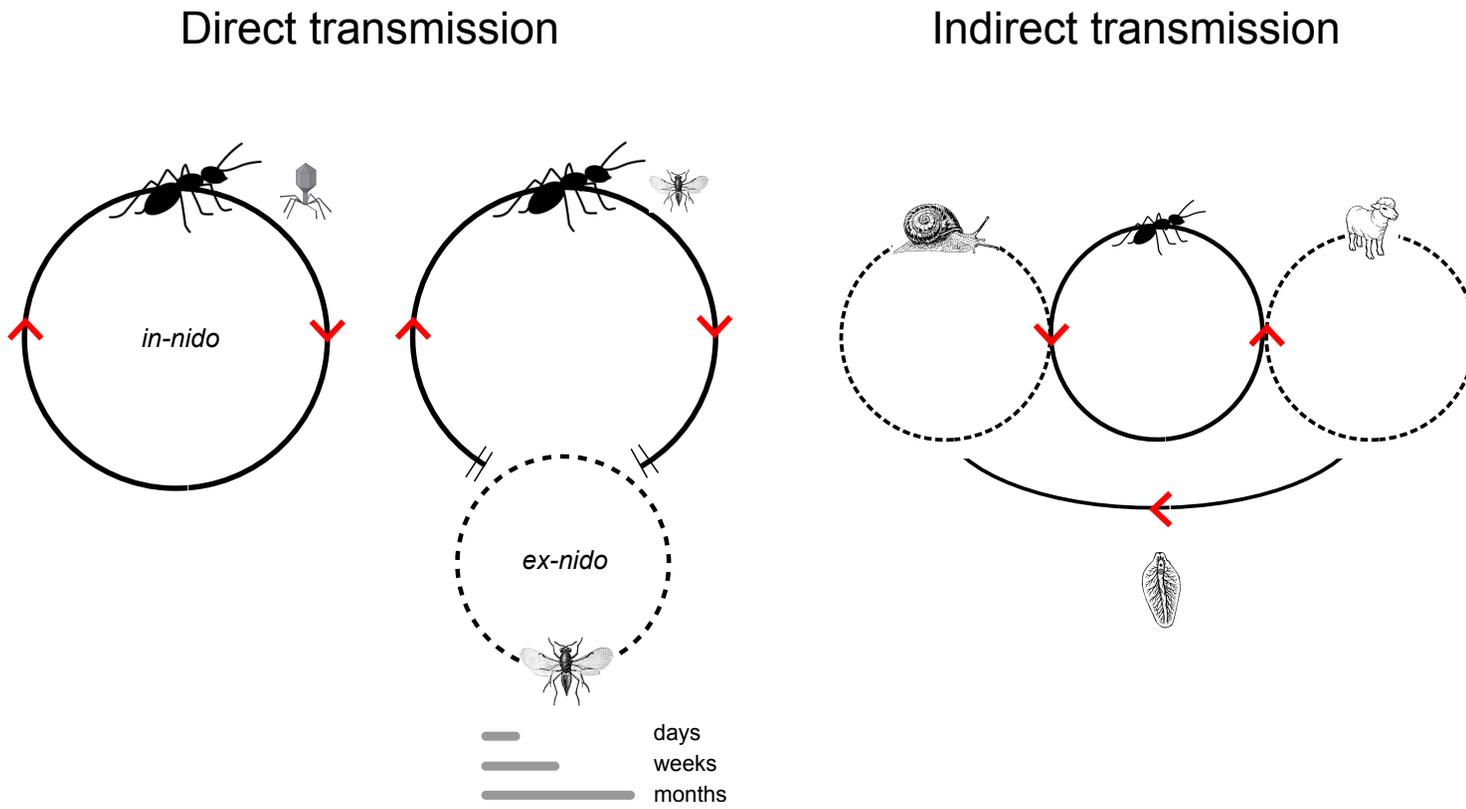


Figure 2.3: Schema of literature search for parasite records.

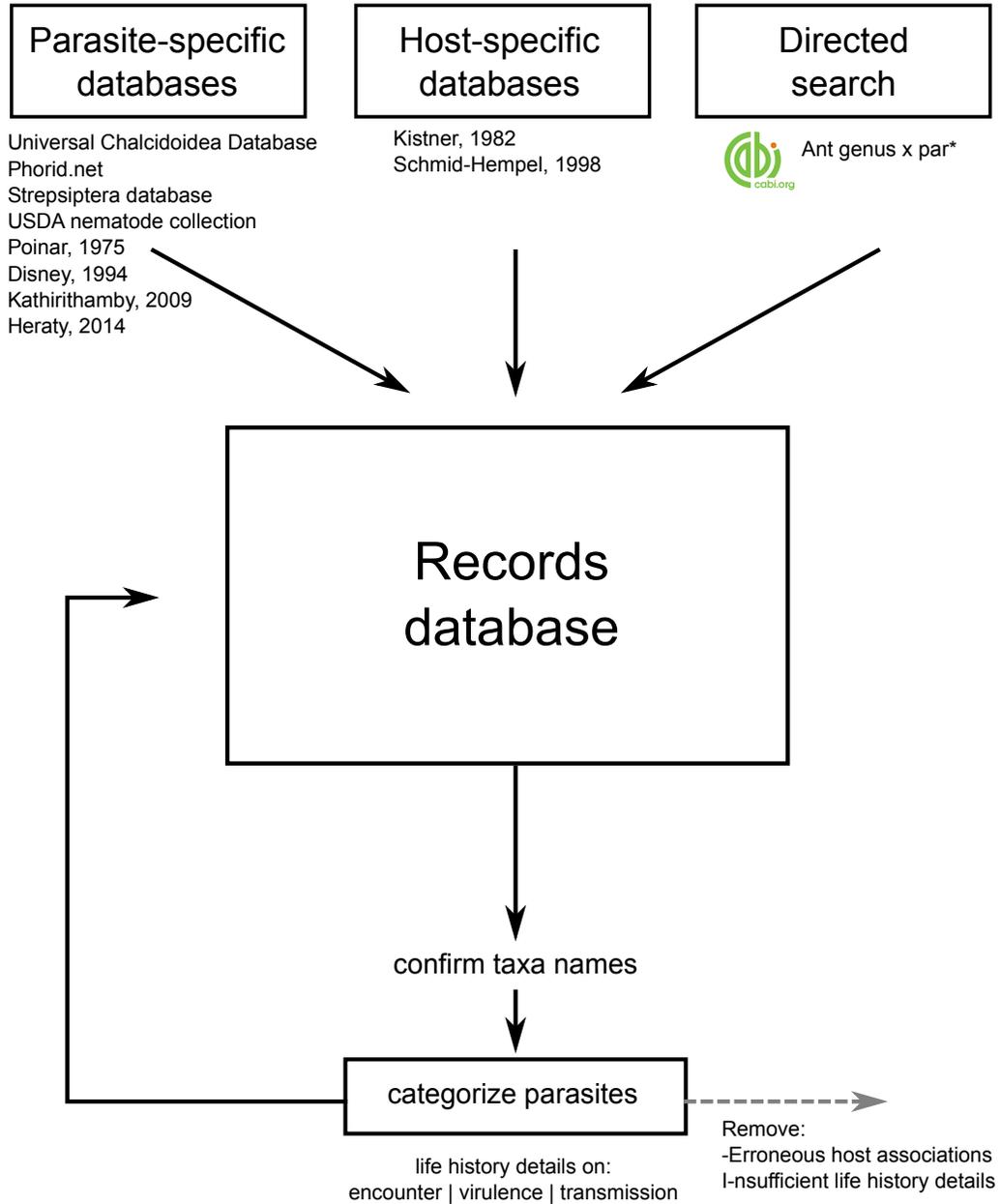


Figure 2.4: Host relationship (associates and parasites) across all parasite groups.

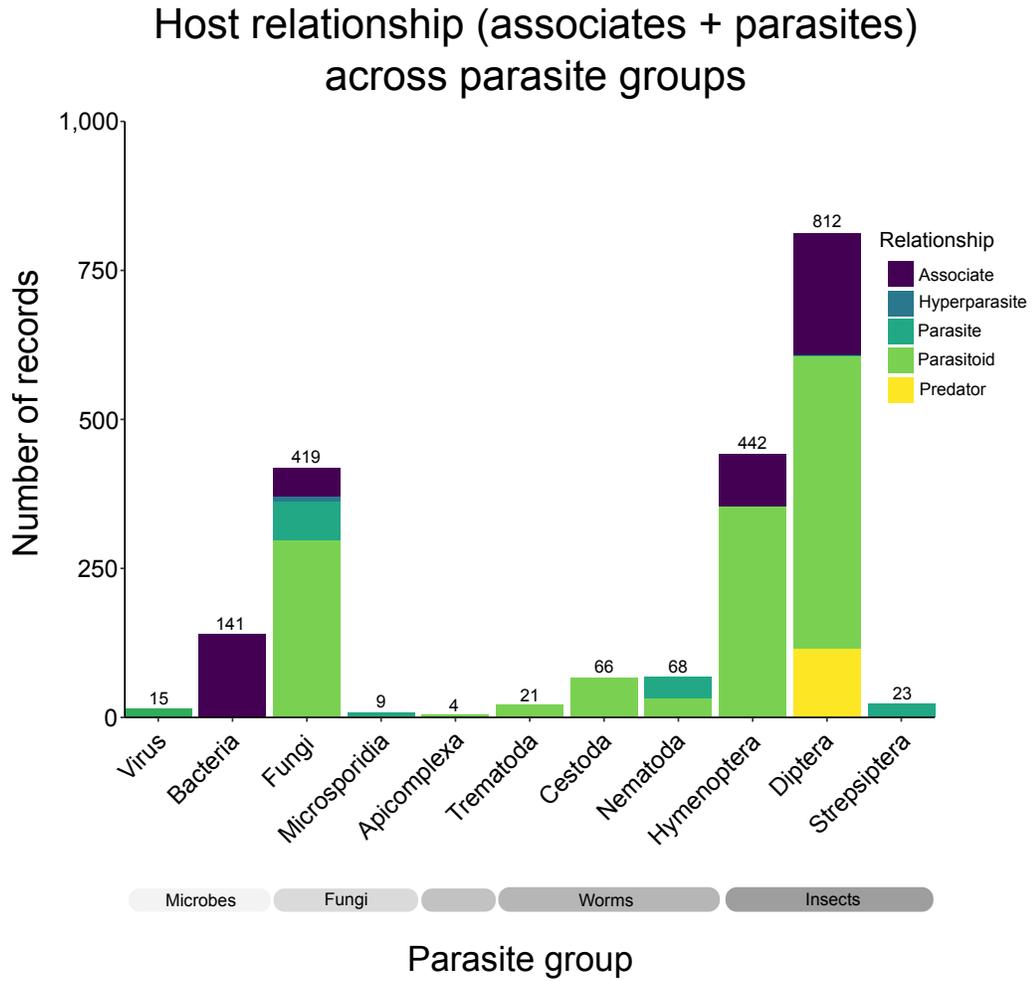


Figure 2.5: Parasites and parasitoids: number of records by parasite group.

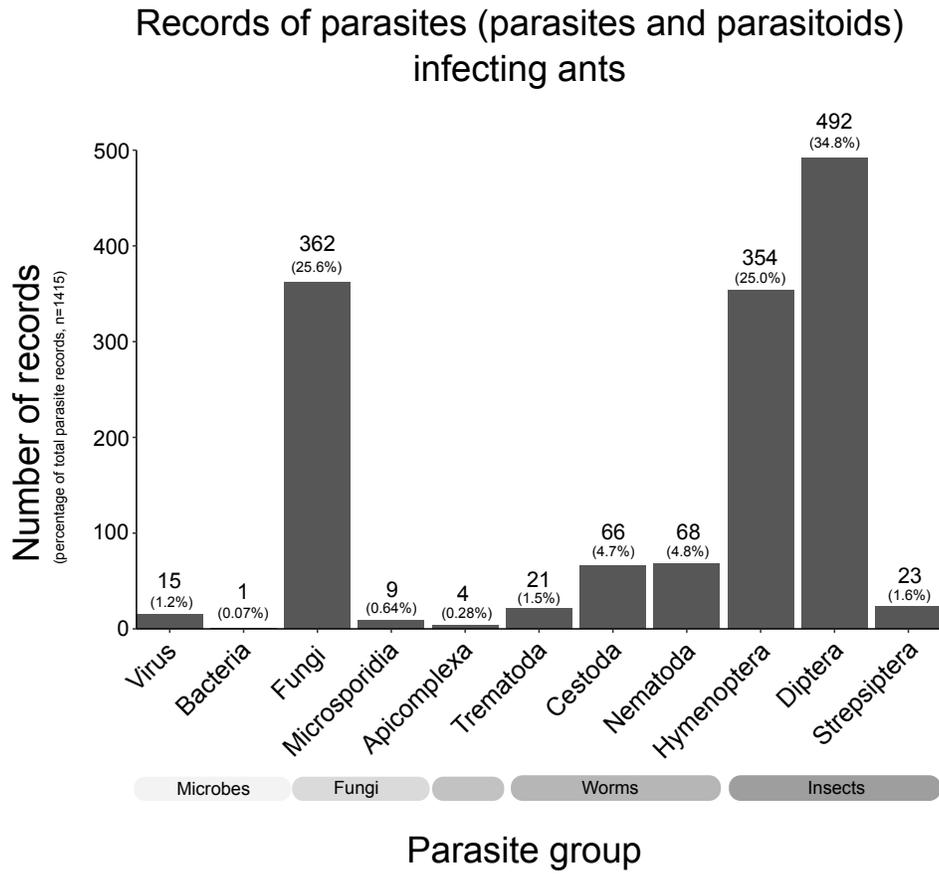


Figure 2.6: Parasites and parasitoids: host relationship by parasite group.

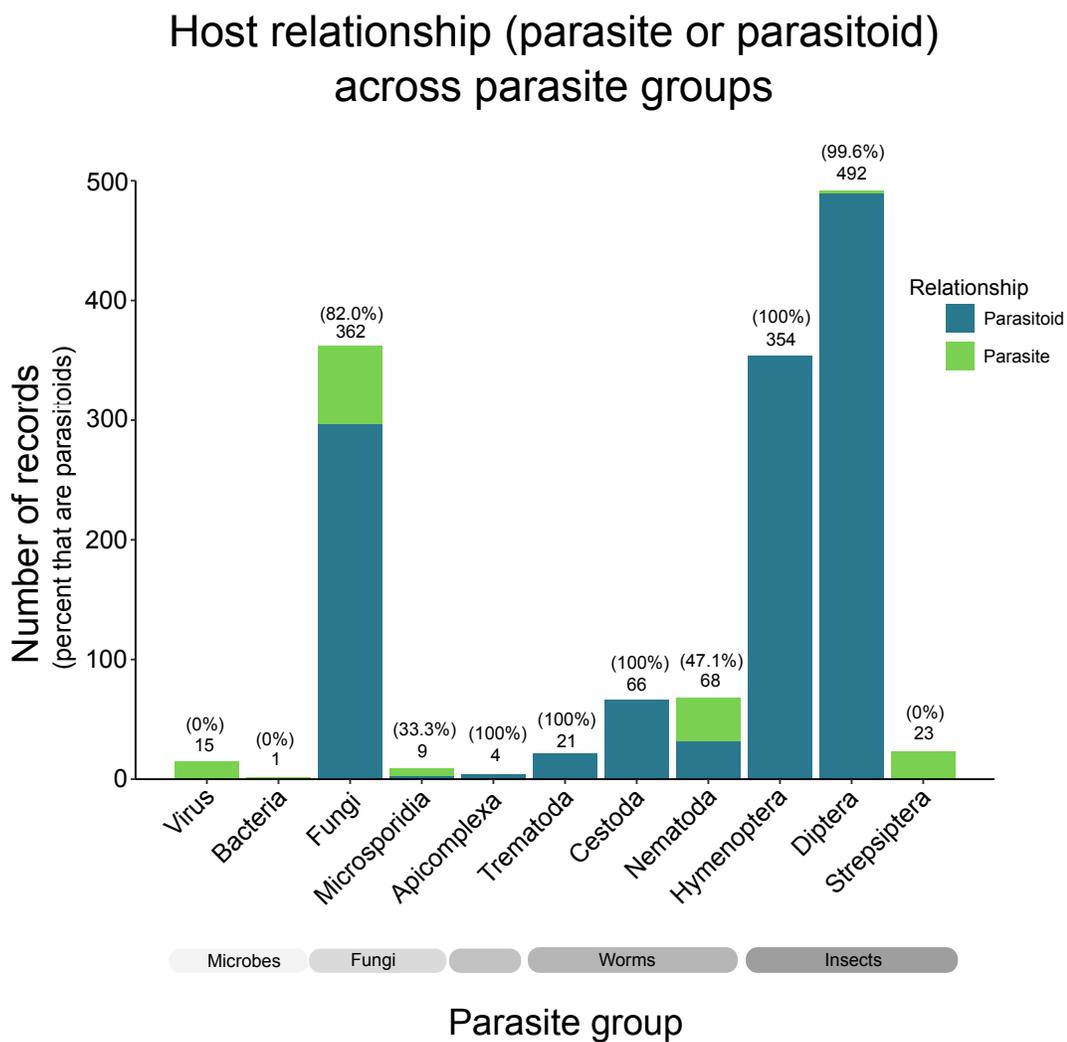


Figure 2.7: Parasites and parasitoids: encounter mode by parasite group.

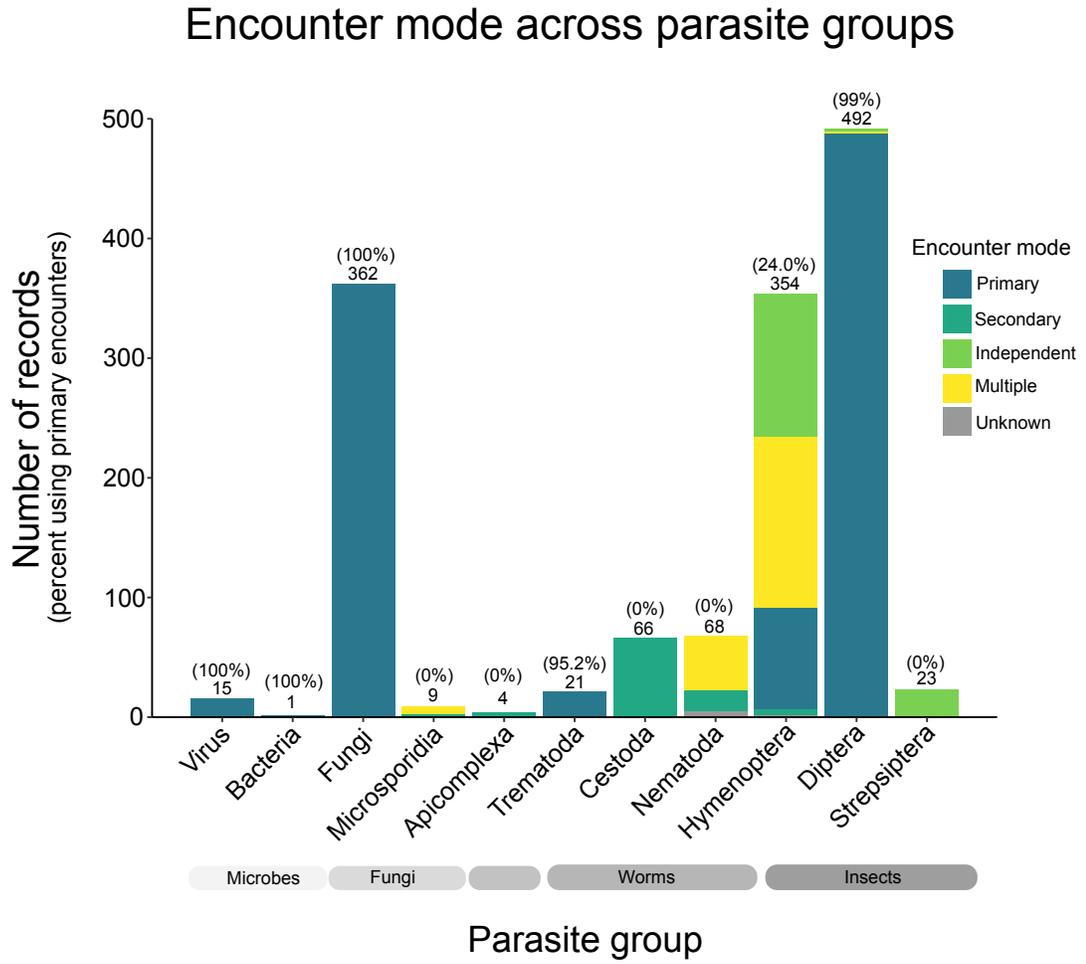


Figure 2.8: Parasites and parasitoids: transmission mode by parasite group.

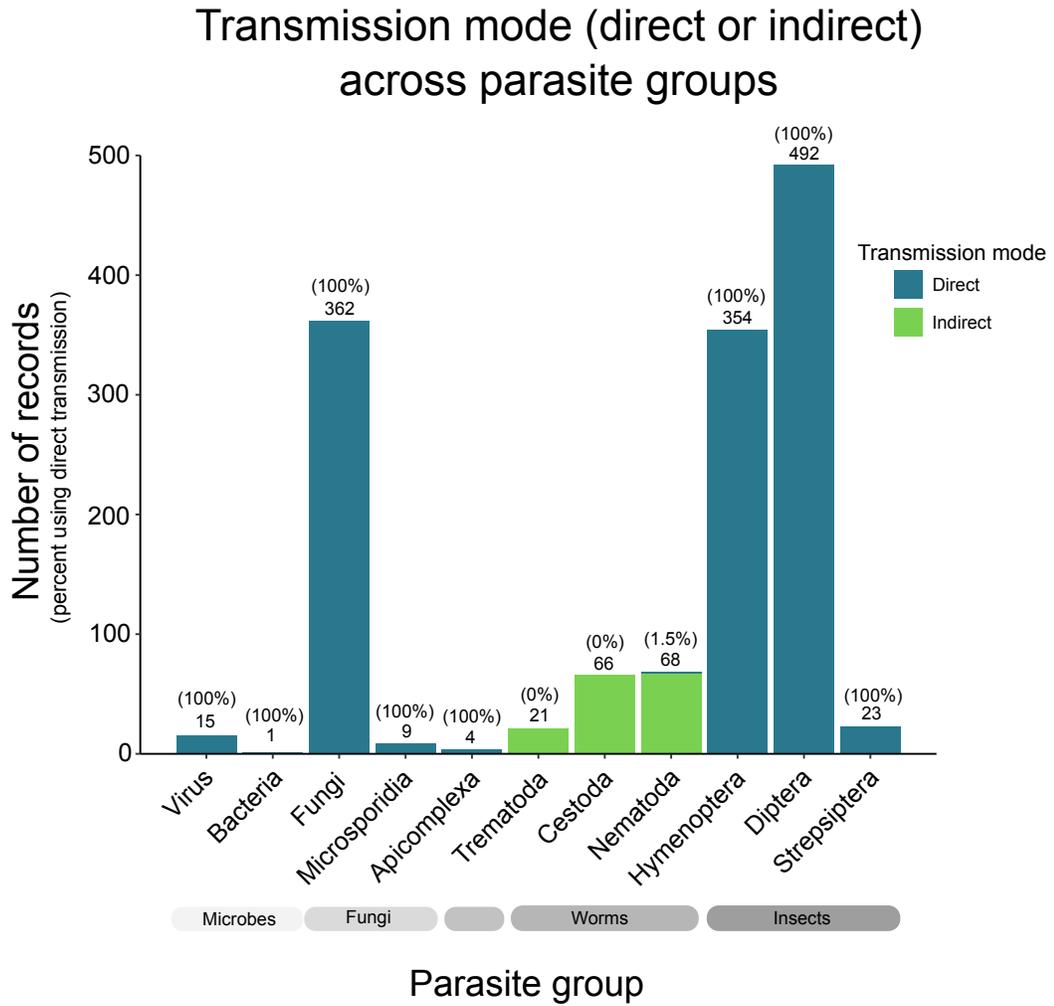


Figure 2.9: Parasites and parasitoids: transmission location by parasite group.

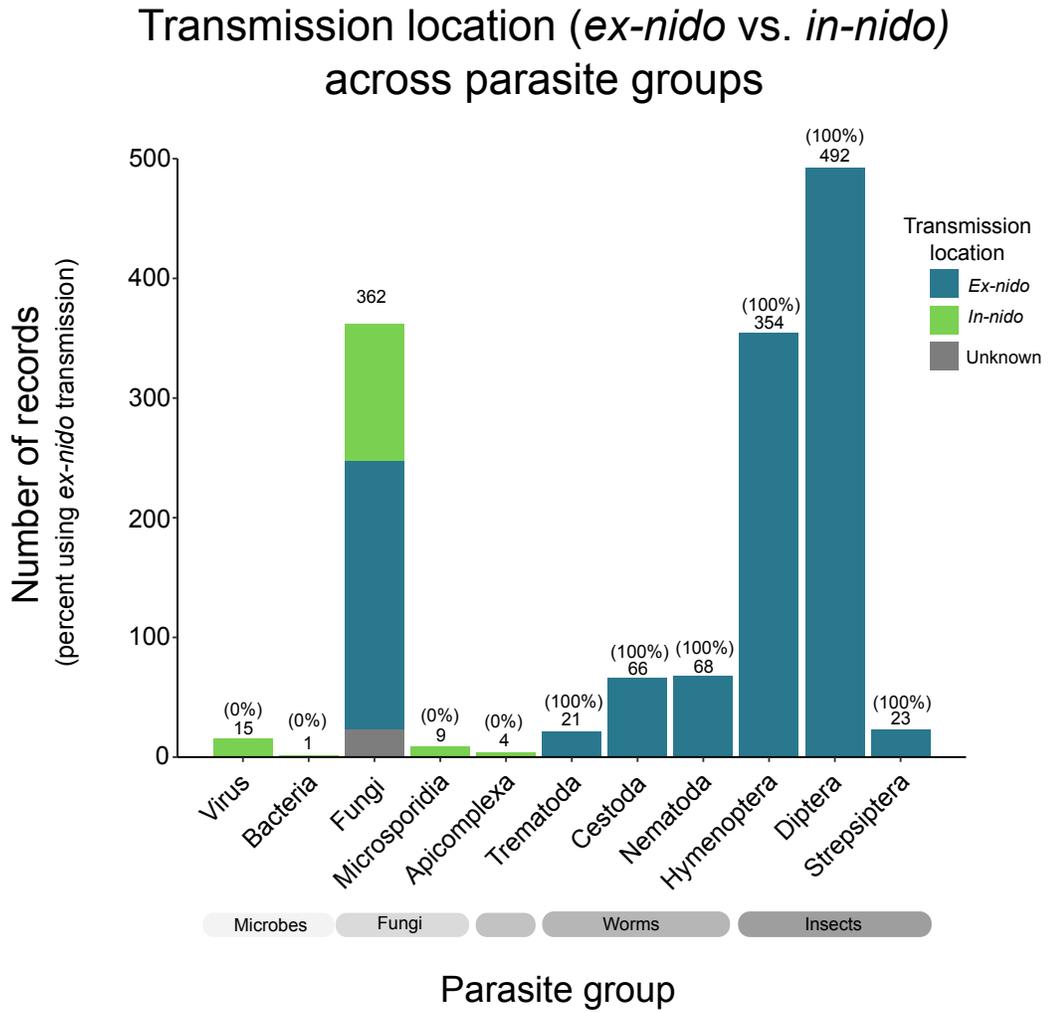


Figure 2.10: Parasites and parasitoids: host location by parasite group.

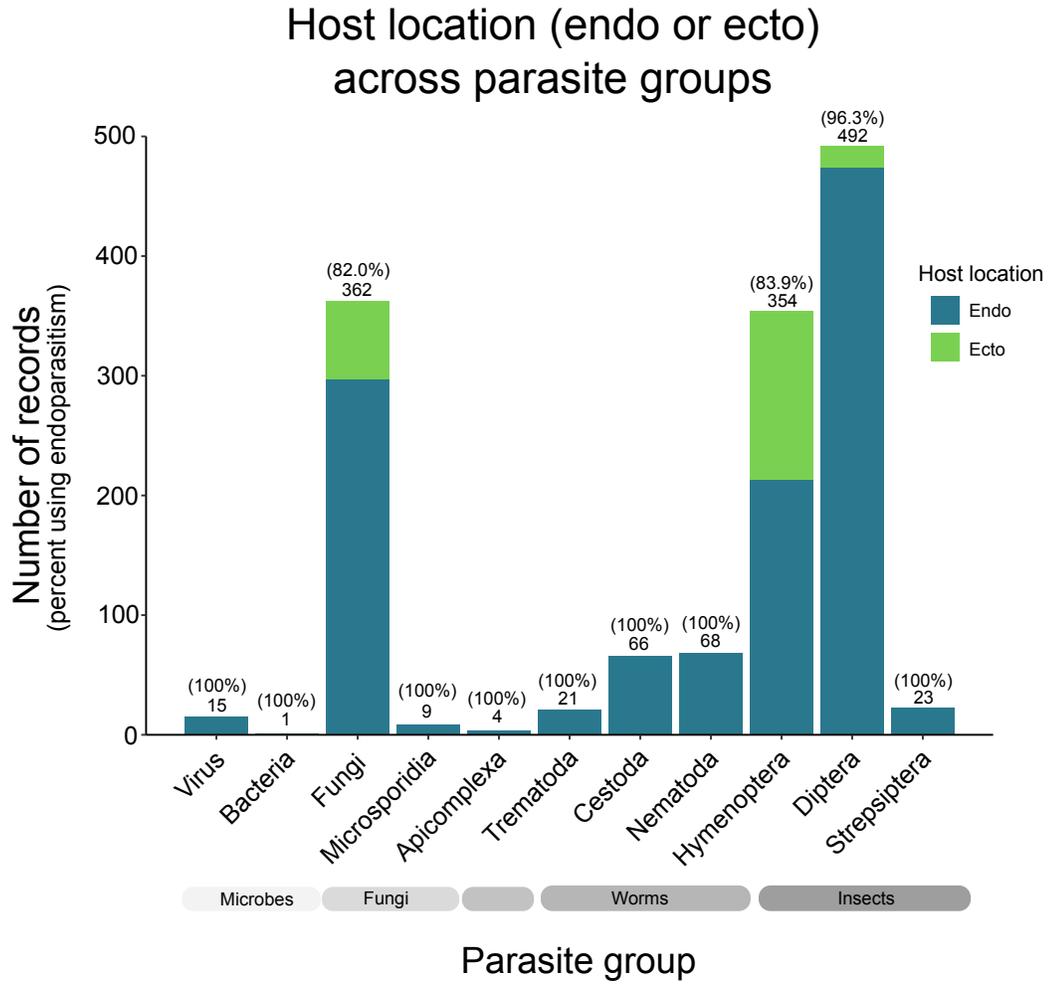


Figure 2.11: Parasites and parasitoids: co-association of relationship and transmission location.

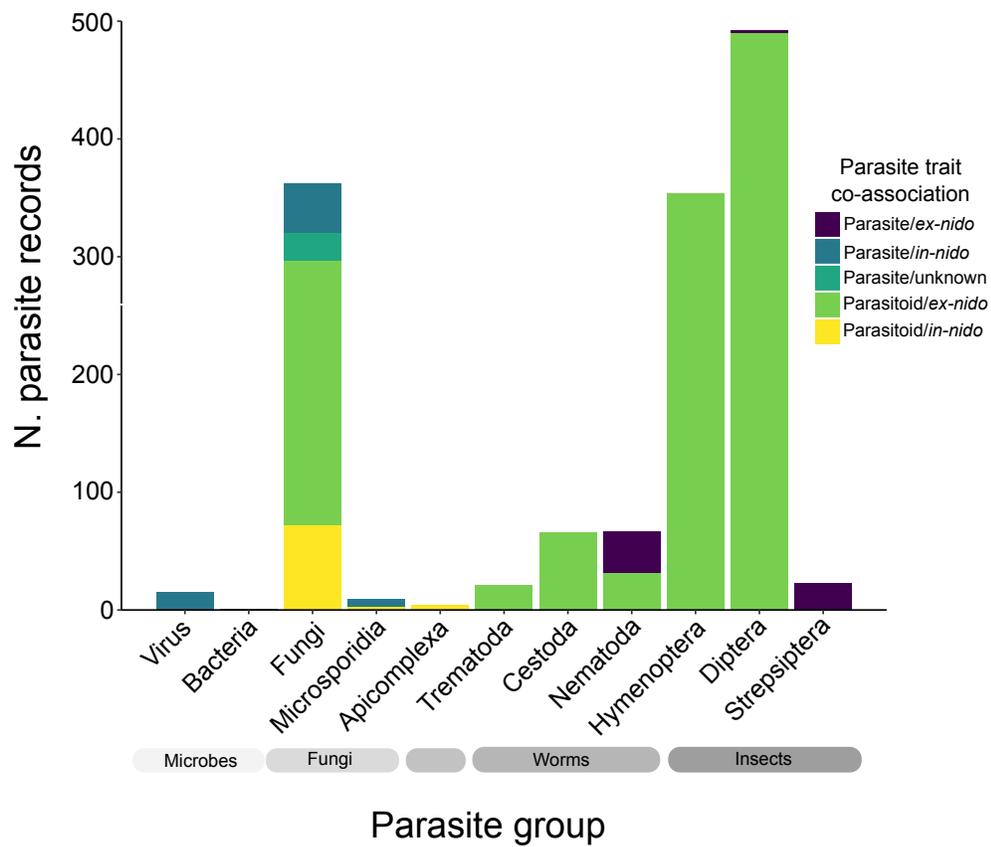
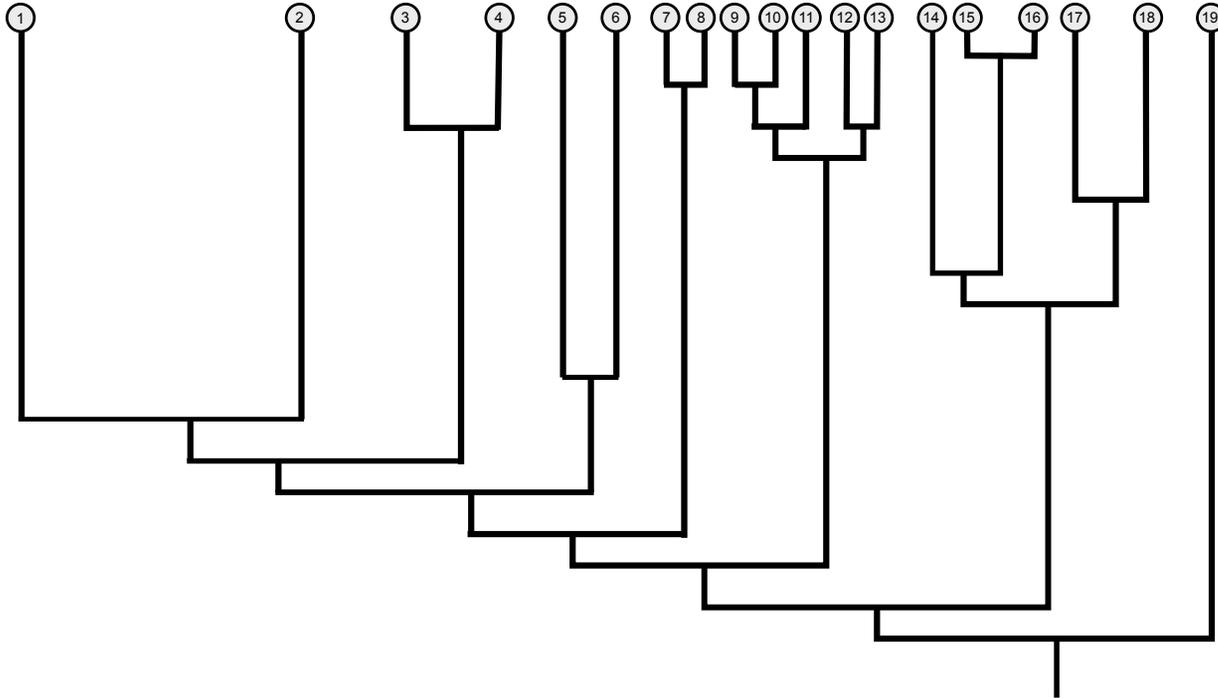


Figure 2.12: Parasite records across ant subfamilies.

	743	647	50	0	105	0	7	14	0	158	118	0	0	168	0	10	0	0	0
Strepsiptera	■	■	□	□	■	□	■	□	□	■	■	□	□	■	□	□	□	□	□
Diptera	■	■	■	□	■	□	■	□	□	■	■	□	□	■	□	■	□	□	□
Hymenoptera	■	■	■	□	■	□	■	■	□	■	■	□	□	■	□	□	□	□	□
Nematoda	■	■	■	□	■	□	□	□	□	■	□	□	□	■	□	□	□	□	□
Helminths	■	■	□	□	■	□	□	□	□	□	□	□	□	■	□	□	□	□	□
Fungi	■	■	■	□	■	□	■	■	□	■	□	□	□	■	□	■	□	□	□
Bacteria	■	■	□	□	■	□	□	□	□	□	□	□	□	□	□	□	□	□	□
Viruses	■	■	□	□	■	□	□	□	□	□	□	□	□	□	□	□	□	□	□



- | | | | | | | |
|------------------|--------------------|---------------------|----------------|----------------------|-----------------------|-------------------|
| Ant sub-families | 2. Formicinae | 5. Dolichoderinae | 8. Myrmeciinae | 11. Ecitoninae | 14. Ponerinae | 17. Amblyoponinae |
| 1. Myrmicinae | 3. Ectatomminae | 6. Aneuretinae | 9. Aenictinae | 12. Cerapachyinae | 15. Agroecomyrmecinae | 18. Proceratiinae |
| | 4. Heteroponerinae | 7. Pseudomyrmecinae | 10. Dorylinae | 13. Leptanilloidinae | 16. Paraponerinae | 19. Leptanillinae |

Figure 2.14: Histogram of number of parasite records by ant genus.

Histogram of number of parasite records

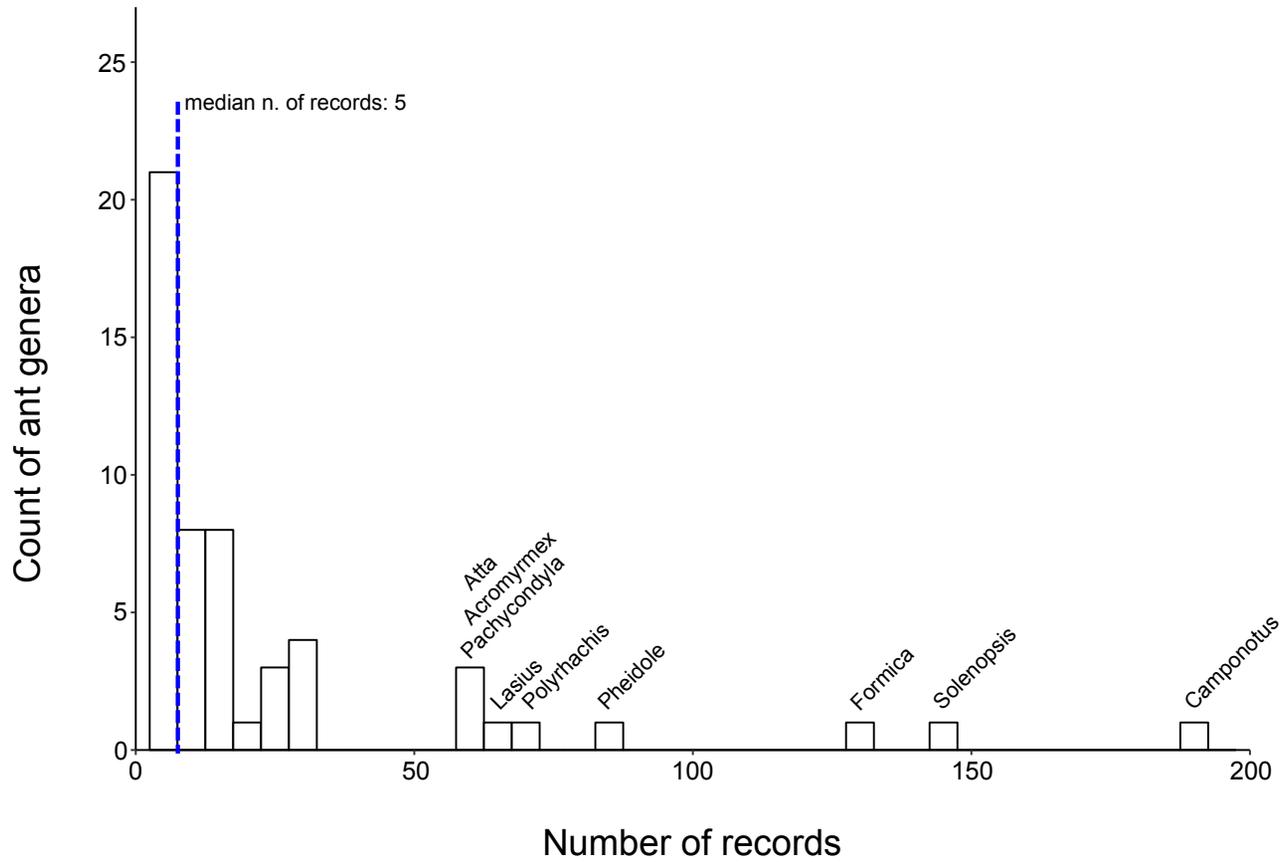


Figure 2.15: Number of parasite records as a function of the number of species in an ant genus.

Number of parasites records found for a given genus as a function of the number of ant species in that genus. The blue line represents a simple linear regression fit of n . records n . host species.

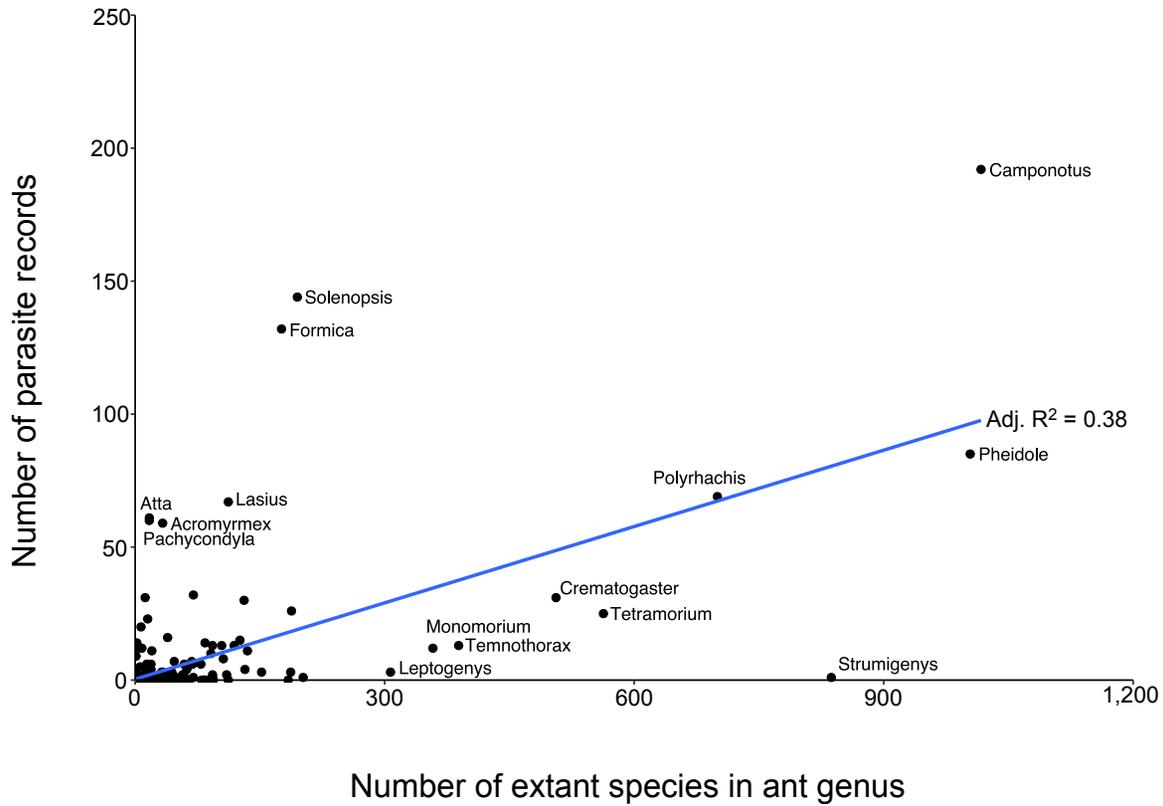


Table 2.1: Defining terms of host association and parasite life history

Defining host associations		
Term	N. hosts per lifestage	Host death/castration as developmental necessity
Parasite	1	no
Parasitoid	1	yes
Predator	> 1	yes
Social parasites	> 1	no
Additional definitions of parasite life history traits		
Direct transmission	Parasitic organisms only require 1 host to complete life cycle.	
Indirect transmission	Parasitic organisms require 2 ⁺ hosts to complete life cycle.	
<i>Ex-nido</i> transmission	Parasitic organisms need to leave nest before transmission to next ant host.	
<i>In-nido</i> transmission	Parasitic organisms can transmit between ant hosts without leaving the nest.	

Table 2.2: Summary of parasite records by parasite family

Parasite records by parasite family						
Parasite group	Parasite family	Total n. records	N. parasite genera	N. parasite species	N. host genera	N. host species
Virus	Dicistroviridae	7	3	4	2	5
-	Iflaviridae	1	1	1	1	1
-	IncertaeSedis	2	1	1	2	2
-	Parvoviridae	1	1	1	1	1
-	Picornaviridae	2	1	1	1	2
-	Solinviviridae	2	1	1	1	2
Bacteria	Pseudomonadaceae	1	1	1	1	1
Fungi	Ancylistaceae	1	1	1	1	1
-	Clavicipitaceae	7	1	2	5	6
-	Cordycipitaceae	31	2	2	18	31
-	Entomophthoraceae	13	2	3	3	9
-	<i>Incertae Sedis</i>	65	3	7	21	63
-	Laboulbeniaceae	39	2	4	8	37

Continuation of Table 2.2

Parasite group	Parasite family	Total n. records	N. parasite genera	N. parasite species	N. host genera	N. host species
-	Ophiocordycipitaceae	197	4	54	28	121
-	Pleosporaceae	1	1	1	1	1
-	Trichocomaceae	8	1	1	6	8
Microsporidia	Burenellidae	5	2	2	1	5
-	<i>Incertae Sedis</i>	4	1	1	1	4
Apicomplexa	Lipotrophidae	4	1	2	2	3
Trematoda	Dicrocoeliidae	20	2	4	4	19
-	Heterophyidae	1	1	1	1	1
Cestoda	Davaineidae	62	2	18	12	40
-	Dilepididae	2	2	2	1	2
-	Mesocestoididae	2	1	1	2	2
Nematoda	Allantonematidae	2	2	2	2	2
-	Diplogastridae	2	2	2	2	2
-	Heterorhabditae	2	1	1	1	2
Nematoda	Mermithidae	17	8	13	10	13

Continuation of Table 2.2

Parasite group	Parasite family	Total n. records	N. parasite genera	N. parasite species	N. host genera	N. host species
-	Panagrolaimidae	2	1	1	2	2
-	Physalopteridae	1	1	1	1	1
-	Rhabditidae	30	9	11	13	19
-	Seuratidae	1	1	1	1	1
-	Steinernematidae	8	1	1	5	8
-	Tetradonematidae	3	2	3	2	3
Hymenoptera	Braconidae	47	4	16	6	33
-	Chalcididae	5	1	5	1	1
-	Diapriidae	38	8	27	8	15
-	Encyrtidae	1	1	1	1	1
-	Eucharitidae	199	29	109	30	132
-	Eulophidae	12	3	7	3	11
-	Eupelmidae	2	1	2	2	2
-	Eurytomidae	10	1	3	2	8
Hymenoptera	Ichneumonidae	33	4	8	4	17
-	Mutilidae	5	1	5	1	1

Continuation of Table 2.2

Parasite group	Parasite family	Total n. records	N. parasite genera	N. parasite species	N. host genera	N. host species
-	Pteromalidae	2	1	1	1	2
Diptera	Chloropidae	1	1	1	1	1
-	Ephydriidae	2	1	2	1	1
-	Helosciomyzidae	1	1	1	1	1
-	Phoridae	485	32	262	40	182
-	Syrphidae	1	1	1	1	1
-	Tachinidae	2	1	1	1	2
Strepsiptera	Myrmecolacidae	23	3	12	9	22
	Total	1415	160	616	-	-

End of Table 2.2

Table 2.3: Summary of parasite life history traits by parasite family

Life history traits by parasite family									
Parasite group	Parasite family	Total n. records	% Primary	% Secondary	% Independent	% Multiple	% Direct	% Ex-nido	% Endo
Virus	Dicistroviridae	7	100	0	0	0	100	0	100
-	Iflaviridae	1	100	0	0	0	100	0	100
-	IncertaeSedis	2	100	0	0	0	100	0	100
-	Parvoviridae	1	100	0	0	0	100	0	100
-	Picornaviridae	2	100	0	0	0	100	0	100
-	Soliniviridae	2	100	0	0	0	100	0	100
Bacteria	Pseudomonadaceae	1	100	0	0	0	100	0	100
Fungi	Ancylistaceae	1	100	0	0	0	100	0	100
-	Clavicipitaceae	7	100	0	0	0	100	0	100
-	Cordycipitaceae	31	100	0	0	0	100	45.2	100
-	Entomophthoraceae	13	100	0	0	0	100	100	100
-	<i>Incertae Sedis</i>	65	100	0	0	0	100	0	60
-	Laboulbeniaceae	39	100	0	0	0	100	0	0
Fungi	Ophiocordycipitaceae	197	100	0	0	0	100	100	100

Continuation of Table 2.3

Parasite group	Parasite family	Total n. records	% Primary	% Secondary	% Independent	% Multiple	% Direct	% Ex-nido	% Endo
-	Pleosporaceae	1	100	0	0	0	100	100	100
-	Trichocomaceae	8	100	0	0	0	100	0	100
Microsporidia	Burenellidae	5	0	60	0	40	100	0	100
-	<i>Incertae Sedis</i>	4	0	0	0	100	100	0	100
Apicomplexa	Lipotrophidae	4	0	100	0	0	100	0	100
Trematoda	Dicrocoeliidae	20	95	5	0	0	0	100	100
-	Heterophyidae	1	100	0	0	0	0	100	100
Cestoda	Davaineidae	62	0	100	0	0	0	100	100
-	Dilepididae	2	0	100	0	0	0	100	100
-	Mesocestoididae	2	0	100	0	0	0	100	100
Nematoda	Allantonematidae	2	0	50	0	0	50	100	100
-	Diplogastridae	2	0	0	0	100	0	100	100
-	Heterorhabditae	2	0	0	0	100	0	100	100
-	Mermithidae	17	0	88.2	0	0	0	100	100
Nematoda	Panagrolaimidae	2	0	0	0	100	0	100	100

Continuation of Table 2.3

Parasite group	Parasite family	Total n. records	% Primary	% Secondary	% Independent	% Multiple	% Direct	% Ex-nido	% Endo
-	Physalopteridae	1	0	100	0	0	0	100	100
-	Rhabditidae	30	0	0	0	100	0	100	100
-	Seuratidae	1	0	0	0	100	0	100	100
-	Steinernematidae	8	0	0	0	100	0	100	100
-	Tetradonematidae	3	0	33.3	0	0	0	100	100
Hymenoptera	Braconidae	47	100	0	0	0	100	100	100
-	Chalcididae	5	100	0	0	0	100	100	0
-	Diapriidae	38	0	0	100	0	100	100	100
-	Encyrtidae	1	0	100	0	0	100	100	100
-	Eucharitidae	199	0	2	33.2	64.8	100	100	38.2
-	Eulophidae	12	0	0	0	100	100	100	50
-	Eupelmidae	2	0	0	0	100	100	100	0
-	Eurytomidae	10	0	0	100	0	100	100	100
-	Ichneumonidae	33	100	0	0	0	100	100	100
-	Mutilidae	5	0	0	100	0	100	100	0
Hymenoptera	Pteromalidae	2	0	0	0	0	100	100	100

Continuation of Table 2.3

Parasite group	Parasite family	Total n. records	% Primary	% Secondary	% Independent	% Multiple	% Direct	% Ex-nido	% Endo
Diptera	Chloropidae	1	0	0	0	0	100	100	0
-	Ephydriidae	2	100	0	0	0	100	100	0
-	Helosciomyzidae	1	0	0	100	0	100	100	0
-	Phoridae	485	99.6	0	0	0.4	100	100	97.3
-	Syrphidae	1	0	0	100	0	100	100	0
-	Tachinidae	2	100	0	0	0	100	100	100
Strepsiptera	Myrmecolacidae	23	0	0	100	0	100	100	100

End of Table 2.3

Table 2.4: Summary of parasites and parasitoids by ant subfamily

Records of parasites and parasitoids in each parasite group												
Ant subfamily	Total n. records	Virus	Bacteria	Fungi	Microsporidia	Apicomplexa	Trematoda	Cestoda	Nematoda	Hymenoptera	Diptera	Strepsiptera
Dolichoderinae	83	4	0	21	0	0	1	2	5	14	35	1
Dorylinae	55	0	0	2	0	0	0	0	0	1	52	0
Ecitoninae	31	0	0	0	0	0	0	0	1	4	25	1
Ectatomminae	48	0	0	3	0	0	0	0	2	32	11	0
Formicinae	522	2	0	217	0	0	20	4	31	137	102	9
Myrmeciinae	13	0	0	1	0	0	0	0	0	12	0	0
Myrmicinae	520	9	1	81	9	4	0	58	27	119	203	9
Paraponerinae	9	0	0	4	0	0	0	0	0	0	5	0
Ponerinae	128	0	0	30	0	0	0	2	1	34	59	2
Pseudomyrmecinae	5	0	0	3	0	0	0	0	0	1	0	1

Table 2.5: Summary of parasites and parasitoids by ant genus

		Records of parasites and parasitoids by parasite group											
Ant subfamily	Ant genus	Total n. records	Virus	Bacteria	Fungi	Microsporidia	Apicomplexa	Trematoda	Cestoda	Nematoda	Hymenoptera	Diptera	Strepsiptera
Dolichoderinae	<i>Azteca</i>	14	0	0	0	0	0	0	0	2	9	3	0
	<i>Dolichoderus</i>	30	0	0	8	0	0	0	0	0	0	21	1
	<i>Iridomyrmex</i>	6	0	0	0	0	0	0	1	1	0	4	0
	<i>Linepithema</i>	11	4	0	0	0	0	0	0	2	1	4	0
	<i>Dorymyrmex</i>	1	0	0	0	0	0	0	0	0	0	1	0
	<i>Liometopum</i>	1	0	0	0	0	0	0	0	0	0	1	0
	<i>Tapinoma</i>	6	0	0	2	0	0	0	1	0	2	1	0
	<i>Technomyrmex</i>	2	0	0	1	0	0	1	0	0	0	0	0
	<i>Temnothorax</i>	13	0	0	11	0	0	0	0	0	0	2	0
Dorylinae	<i>Dorylus</i>	6	0	0	2	0	0	0	0	0	0	4	0
	<i>Labidus</i>	20	0	0	0	0	0	0	0	0	0	20	0
	<i>Neivamyrmex</i>	15	0	0	0	0	0	0	0	0	1	14	0
	<i>Nomamyrmex</i>	14	0	0	0	0	0	0	0	0	0	14	0
Ecitoninae	<i>Eciton</i>	31	0	0	0	0	0	0	0	1	4	25	1

Continuation of Table 2.5

Ant subfamily	Ant genus	Total n. records	Virus	Bacteria	Fungi	Microsporidia	Apicomplexa	Trematoda	Cestoda	Nematoda	Hymenoptera	Diptera	Strepsiptera
Ectatomminae	<i>Ectatomma</i>	23	0	0	1	0	0	0	0	2	12	8	0
	<i>Gnamptogenys</i>	11	0	0	2	0	0	0	0	0	6	3	0
	<i>Rhytidoponera</i>	13	0	0	0	0	0	0	0	0	13	0	0
	<i>Typhlomyrmex</i>	1	0	0	0	0	0	0	0	0	1	0	0
Formicinae	<i>Camponotus</i>	192	1	0	70	0	0	3	0	6	31	73	8
	<i>Cataglyphis</i>	10	0	0	2	0	0	2	0	0	6	0	0
	<i>Cladomyrma</i>	2	0	0	0	0	0	0	0	2	0	0	0
	<i>Formica</i>	132	1	0	43	0	0	14	1	5	58	10	0
	<i>Lasius</i>	67	0	0	16	0	0	1	1	16	24	9	0
	<i>Myrmecocystus</i>	2	0	0	1	0	0	0	0	0	1	0	0
	<i>Myrmelachista</i>	1	0	0	0	0	0	0	0	0	0	0	1
	<i>Polyergus</i>	6	0	0	3	0	0	0	0	0	3	0	0
	<i>Prenolepis</i>	4	0	0	1	0	0	0	2	1	0	0	0
	<i>Prolasius</i>	1	0	0	0	0	0	0	0	1	0	0	0
	<i>Acropyga</i>	2	0	0	0	0	0	0	0	0	0	2	0
Formicinae	<i>Anoplolepis</i>	1	0	0	0	0	0	0	0	0	1	0	0

Continuation of Table 2.5

Ant subfamily	Ant genus	Total n. records												
			Virus	Bacteria	Fungi	Microsporidia	Apicomplexa	Trematoda	Cestoda	Nematoda	Hymenoptera	Diptera	Strepsiptera	
	<i>Calomyrmex</i>	1	0	0	0	0	0	0	0	0	0	1	0	0
	<i>Echinopla</i>	3	0	0	3	0	0	0	0	0	0	0	0	0
	<i>Euprenolepis</i>	1	0	0	0	0	0	0	0	0	0	0	1	0
	<i>Nylanderia</i>	2	0	0	1	0	0	0	0	0	0	0	1	0
	<i>Oecophylla</i>	12	0	0	7	0	0	0	0	0	0	5	0	0
	<i>Paratrechina</i>	5	0	0	2	0	0	0	0	0	0	1	2	0
	<i>Phasmomyrmex</i>	4	0	0	4	0	0	0	0	0	0	0	0	0
	<i>Plagiolepis</i>	4	0	0	3	0	0	0	0	0	0	1	0	0
	<i>Polyrhachis</i>	69	0	0	61	0	0	0	0	0	0	5	3	0
	<i>Pseudolasius</i>	1	0	0	0	0	0	0	0	0	0	0	1	0
Myrmeciinae	<i>Myrmecia</i>	13	0	0	1	0	0	0	0	0	0	12	0	0
Myrmicinae	<i>Acromyrmex</i>	59	0	0	3	0	0	0	0	0	2	7	47	0
	<i>Aphaenogaster</i>	3	0	0	2	0	0	0	0	0	0	0	1	0
	<i>Atta</i>	61	0	0	8	0	0	0	0	0	2	0	51	0
	<i>Crematogaster</i>	31	0	0	14	0	0	0	0	1	2	4	8	2
Myrmicinae	<i>Messor</i>	8	0	0	2	0	0	0	0	0	0	6	0	0

Continuation of Table 2.5

Ant subfamily	Ant genus	Total n. records												
			Virus	Bacteria	Fungi	Microsporidia	Apicomplexa	Trematoda	Cestoda	Nematoda	Hymenoptera	Diptera	Strepsiptera	
	<i>Myrmica</i>	26	0	0	12	0	0	0	0	2	2	6	4	0
	<i>Pheidole</i>	85	0	0	4	0	0	0	0	24	0	42	11	4
	<i>Pogonomyrmex</i>	7	0	0	2	0	0	0	0	0	2	3	0	0
	<i>Solenopsis</i>	144	9	1	12	9	3	0	1	12	12	24	70	3
	<i>Tetramorium</i>	25	0	0	6	0	0	0	0	17	1	1	0	0
	<i>Apterostigma</i>	3	0	0	0	0	0	0	0	0	0	0	3	0
	<i>Cardiocondyla</i>	1	0	0	1	0	0	0	0	0	0	0	0	0
	<i>Carebara</i>	1	0	0	0	0	0	0	0	0	0	0	1	0
	<i>Cephalotes</i>	13	0	0	5	0	0	0	0	0	4	0	4	0
	<i>Cyphomyrmex</i>	16	0	0	0	0	0	0	0	0	0	16	0	0
	<i>Daceton</i>	2	0	0	1	0	0	0	0	0	0	0	1	0
	<i>Goniomma</i>	1	0	0	1	0	0	0	0	0	0	0	0	0
	<i>Leptothorax</i>	4	0	0	0	0	1	0	0	2	0	1	0	0
	<i>Macromischoides</i>	4	0	0	4	0	0	0	0	0	0	0	0	0
	<i>Monomorium</i>	12	0	0	0	0	0	0	0	10	0	1	1	0
Myrmicinae	<i>Pheidologeton</i>	2	0	0	0	0	0	0	0	1	0	0	1	0
	<i>Strongylognathus</i>	1	0	0	1	0	0	0	0	0	0	0	0	0

Continuation of Table 2.5

Ant subfamily	Ant genus	Total n. records	Virus	Bacteria	Fungi	Microsporidia	Apicomplexa	Trematoda	Cestoda	Nematoda	Hymenoptera	Diptera	Strepsiptera
	<i>Strumigenys</i>	1	0	0	1	0	0	0	0	0	0	0	0
	<i>Trachymyrmex</i>	7	0	0	1	0	0	0	0	0	6	0	0
	<i>Wasmannia</i>	2	0	0	0	0	0	0	0	0	2	0	0
Paraponerinae	<i>Paraponera</i>	9	0	0	4	0	0	0	0	0	0	5	0
Ponerinae	<i>Pachycondyla</i>	60	0	0	18	0	0	0	1	0	7	32	2
	<i>Bothroponera</i>	1	0	0	1	0	0	0	0	0	0	0	0
	<i>Brachyponera</i>	6	0	0	0	0	0	0	1	0	5	0	0
	<i>Diacamma</i>	3	0	0	2	0	0	0	0	0	1	0	0
	<i>Dinoponera</i>	12	0	0	1	0	0	0	0	0	1	10	0
	<i>Hypoponera</i>	3	0	0	0	0	0	0	0	0	3	0	0
	<i>Leptogenys</i>	3	0	0	1	0	0	0	0	0	0	2	0
	<i>Neoponera</i>	2	0	0	0	0	0	0	0	0	1	1	0
	<i>Odontomachus</i>	32	0	0	1	0	0	0	0	1	16	14	0
	<i>Paltothyreus</i>	4	0	0	4	0	0	0	0	0	0	0	0
Ponerinae	<i>Phrynoponera</i>	1	0	0	1	0	0	0	0	0	0	0	0
	<i>Platythyrea</i>	1	0	0	1	0	0	0	0	0	0	0	0

Continuation of Table 2.5

Ant subfamily	Ant genus	Total n. records	Virus	Bacteria	Fungi	Microsporidia	Apicomplexa	Trematoda	Cestoda	Nematoda	Hymenoptera	Diptera	Strepsiptera
Pseudomyrmecinae	<i>Pseudomyrmex</i>	4	0	0	2	0	0	0	0	0	1	0	1
	<i>Tetraoponera</i>	1	0	0	1	0	0	0	0	0	0	0	0

End of Table 2.5

Modeling the impact of *ex-nido* transmitted parasites on ant colony dynamics

3.1 Abstract

Infectious disease outbreaks are a common constraint of group living organisms. Ants (Hymenoptera: Formicidae) live in large, dense colonies and are host to a diverse range of parasites and pathogens, facilitating the possibility of epidemic-induced collapse. However, the majority of parasites infecting ants require a period of development outside of the nest (*ex-nido*) before they can transmit to their next ant host and the impact of these parasites on colony dynamics is unknown. Here we develop a mathematical model to assess ant colony dynamics in the presence of such parasites. We find that under field-realistic model conditions, these parasites are unlikely to cause the epidemic collapse of mature ant colonies. The preponderance of *ex-nido* transmitting parasites infecting ants and their limited epidemiological impact on colony dynamics may partly explain why collapsed ant colonies are rarely, if ever, observed in natural populations.

3.2 Introduction

Infectious diseases capable of massive mortality events appear to be an unavoidable consequence of living in large, complex societies. As humans evolved from small groups of hunter-gatherers into larger agrarian societies and then cities, we have seen

an increase in the number of outbreaks that our societies experience [399, 400]. Some diseases (i.e. measles, seasonal influenza) are ‘crowd diseases’ that can only be maintained because of large numbers of individuals living in close proximity. Outbreaks readily occur in large natural and managed animal populations as well. Boom-bust cycles in Gypsy moths driven by virus epidemics [401], Ebola and anthrax outbreaks amongst chimpanzees and gorillas [402, 403], and recurrent foot-and-mouth disease epizootics in commercial bovid all demonstrate that high density, group living organisms often contend with the steep costs of intense disease burden.

However, infectious disease outbreaks may not necessarily be an unavoidable consequence of evolving to live in dense groups. Social insects in the order Hymenoptera (ants, bees, and wasps), and the ants in particular, exemplify the living conditions that exaggerate the perceived risk of infectious disease spread. These animal groups are defined by eusociality, the highest form of social organization, in which there is a reproductive division of labor, overlapping generations, and cooperative brood care [38]. Eusociality means that these groups often live in extremely dense living conditions with large colony sizes (up to millions of individuals; [89], reviewed in [88]), and have an average higher genetic relatedness compared to other animal groups. This risk is further compounded by nesting habitats in soil and decaying wood that put colonies at increased risk of contact with microbial loads capable of causing disease [404]. Additionally, neighboring colonies overlap in their foraging ecology and compete for the same food resources, enhancing the potential for inter-colony transmission [5, 405]. Indeed, social insects are host to a diverse range of pathogens, parasites, and parasitoids (hereafter ‘parasites’) [91, 406]. However, ants and other social insects have achieved incredible ecological success [61, 407], and effectively managing their disease burden could be one underlying reason for their continued success over evolutionary time.

Attempting to understand how social insects have contended with considerable parasite pressure over their long evolutionary history has driven empirical research during the past two decades. This work has uncovered many disease-fighting mechanisms that social insects have in their arsenal, including physiological, behavioral, and organizational defenses at both the individual- and colony- levels (reviewed in [91, 97, 99, 127, 129]). Some mechanisms, such as allogrooming (the grooming of nest mates) [136, 408] and the transfer of immune modulators or antibiotic secretions between nest mates [408, 409], are evolutionary innovations following their transition

to eusociality, but it is likely that many of these immune mechanisms were present prior to the transition to eusociality [92].

Complementary theoretical studies have used a variety of modeling frameworks to test the relative efficacies of these mechanisms against parasites that are capable of direct transmission from one infected nest mate to another. For example, deterministic compartmental modeling has been used to assess differences in epidemiological outcomes when passive versus active immune modulators are passed between nest mates [133], and how grooming, a behavioral defense used to remove infectious particles prior to infection, could impact epidemic potential inside colonies [140]. Others have used individual-based modeling approaches to investigate how interaction heterogeneity [154], nest architecture [155], and immunity and hygienic behavior [156] impact disease severity and colony survival. These modeling approaches have been very useful for comparing the relative efficacies of anti-disease defenses against parasites that are capable of transmission inside the nest.

One key assumption underlying most of the above work is that parasites infecting ants are capable of direct, ant-to-ant transmission inside the nest. However, the majority of parasite species that infect ants have lifecycles that require a period of development outside of the colony (*ex-nido*), often as free-living stages or in other host species, before they are able to infect new hosts (Figure 3.1) [91] (Chapter 2). The amount of time such parasites need before they are capable of infecting a new ant host varies considerably, from days to months or even years. For example, following emergence from their ant host, phorid flies must mate and then find new hosts to oviposit into within days [179]. Trematodes infecting ants must complete development inside their vertebrate final host, mate and release eggs to be consumed by a snail before another ant can be infected, a process which can take months [410]. Finally, in temperate systems, the zombie-ant fungus *Ophiocordyceps* does not develop the sexual stages needed to release spores and infect new ants until many months following the death of its original ant host [255]. Thus, with these *ex-nido* parasites, direct transmission between nest mates inside colonies is not possible, potentially precluding the threat of major disease outbreaks inside colonies.

To date, no theoretical studies have investigated the potential impact of *ex-nido* parasites on ant colony dynamics. Here, we formally explore the consequences of *ex-nido* parasites by building a model of ant colony dynamics in the absence of parasite pressure; we then extend it to a ‘susceptible-infected-removed’ (SIR)-type model

for the disease dynamics of parasites transmitted outside of ant colonies. While this model was built to capture ant colony dynamics, it is generally applicable to other social insect colonies. We explore how changing colony birth and parasite transmission rates impact colony dynamics and show that for a range of biological plausible parameter values, colony collapse is unlikely to occur. Finally we explore how other parameters (i.e. proportion of the colony foraging, parasite developmental rate) impact the potential impact of *ex-nido* parasitism on ant colony dynamics. Our work suggests that disease dynamics in ant and other social insect societies, in which *ex-nido* parasitism predominates rather than parasites directly transmitting between nest mates, are fundamentally different from other social living organisms like mammals, which may partly explain the enduring ecological success of the social insects.

3.3 Methods

3.3.1 Model of ant colony dynamics in the presence and absence of *ex-nido* transmitting parasites

Our model of mature ant colony dynamics in the presence and absence of *ex-nido* parasites is given by Eqs. (1-4) and summarized schematically in Fig. 3.2. In the absence of parasitism, we make the simplifying assumption that there are three developmental and sociological castes (compartments) that individuals transition through in ant colonies, listed below:

- **Brood (B)**: a period of biological development during which individuals transition from being eggs through several larval stages.
- **Nest workers (N)**: a variable period of time during which individuals participate in intranidal tasks such as brood care and nest maintenance.
- **Foragers (F_s)**: a variable period of time that older ants transition into according to colony need; foraging ants gather food and participate in extranidal territory defense and maintenance, which puts them at greater risk for both predation and parasitism.

We believe that this captures sufficient biological realism of mature ant colony functioning without over-complicating the model. While some ant species do have

other specialized castes (e.g. soldiers in army ants, repletes in honey pot ants, etc.), the basic colony demographic structure we have selected applies broadly to the majority of ant colonies [5, 58].

Our investigation of colony dynamics in the presence of *ex-nido* parasites, i.e. parasites that require a developmental period outside of the nest before transmission to new hosts, is motivated by the biology of the most prevalent type of ant-infecting parasite that we find from our extensive review of the literature (Chapter 2, parasite records in [22, 91, 179, 182–185], among many others). We model a parasite that encounters and infects a forager ant in the extranidal (outside of the nest) environment, causes the mortality of that ant after some developmental period, and ultimately transmits to its next host in the extranidal environment (i.e. no direct ant-to-ant transmission within the nest). Thus, our model of colony dynamics in the presence of parasitism includes a fourth compartment, **infected foragers** (F_i). When the force of infection term β (described in detail below) is zero, Eqs. (3.1 - 3.3) reduce to the uninfected model, which is used to validate parameter choice and the form of the model. When the force of infection term β is greater than zero, Eqs. (3.1 - 3.4) represent the infected model.

New ants are born into the brood compartment B with colony birth rate λ via a Hill function (see Eq. 3.1), which we assume is dependent on the total colony size and minimum colony size σ needed to maintain colony viability. We choose a Hill function to make the number of brood born into the nest conditional on the total colony size, because workers support brood care by, for example, gathering food resources, feeding larvae, and cleaning brood [5]. Thus, colonies with more workers can support greater numbers of brood. Brood, B, can become nest workers, N, after a developmental period (transitioning at per-capita rate ϕ) or can die due to natural mortality (at per-capita rate μ). We explore a range of colony birthrates to assess the impact of the λ parameter on colony dynamics under the presence of *ex-nido* parasites (Fig. 3.4).

$$\frac{dB}{dt} = \frac{\lambda(F_s + F_i + N + B)^2}{\sigma^2(1 + \frac{(F_s + F_i + N + B)^2}{\sigma^2})} - \phi B - \mu B \quad (3.1)$$

Nest workers can either die due to natural mortality at per-capita rate μ or transition into the forager compartment, F_s , according to colony need. Here we make the assumption that a fixed proportion, κ of the colony is needed for extranidal tasks. We model the nest worker to forager transition using a logistic growth-like term, multi-

plied by the transition rate α , which gives the maximum per-capita transition rate (see Eqs. (2-3)). We explore how sensitive colony population dynamics are to changing this forager proportion κ under the presence of *ex-nido* parasitism in Fig. 3.5. We also perform sensitivity analyses for predicted colony dynamics under changing α in Fig. B.4.

$$\frac{dN}{dt} = \phi B - \alpha N \left(\kappa - \frac{F_s + F_i}{1 + F_s + F_i + N + B} \right) - \mu N \quad (3.2)$$

$$\frac{dF_s}{dt} = \alpha N \left(\kappa - \frac{F_s + F_i}{1 + F_s + F_i + N + B} \right) - \mu F_s - \beta F_s \quad (3.3)$$

Once nest workers become foragers, we make the simplifying assumption that they remain foragers until death, which serves to reduce model complexity. For many ant species, we do not know exactly how workers are allocated to the task of foraging and how much task fidelity these workers exhibit. It is generally assumed that social insect colonies have some degree of temporal polyethism, in which workers age through a sequence of behavioral castes [5, 411] with foraging usually occurring later in life. How workers cycle through tasks over their lifetime likely depends on their physical caste as well [411, 412]. While temporal polyethism gives a general pattern to how individuals cycle through tasks during their lifetime, behavioral flexibility allows colonies to be resilient during catastrophes [413–415], further complicating how colonies are socially organized. For modeling simplicity, we make the assumption that workers follow the traditional series of tasks over their lifetime (interior tasks as nest workers, followed by exterior tasks as foragers) and that foragers remain in that compartment for life. We leave investigation of the impact of behavioral flexibility observed in some colonies on interaction with *ex-nido* parasites for future work.

$$\frac{dF_i}{dt} = \beta F_s - \mu F_i - \gamma F_i \quad (3.4)$$

In the presence of parasitism ($\beta > 0$), susceptible foragers F_s become infected by parasites in the environment at rate β , to become infected foragers F_i (see Eq. 3.4). The per-capita rate β is a parameter that combines the frequency with which foragers leave the nest, their probability of encountering parasites whilst outside the nest, and the probability of successfully becoming infected given an encounter with a parasite. Like their uninfected counterparts, infected foragers F_i can die due to natural mortality μ ; however, they will more likely die a parasite-induced death at rate

γ , which occurs at a more rapid rate (see Table 3.1 for model parameters). Though these infected foragers die at a more rapid rate than their uninfected counterparts, they do not pass on the infection, and in other respects interact with the colony like uninfected foragers. Note that infected foragers are included in the calculation of the total colony size and we assume that there are no infection-related changes in individual or colony-level behavior. In addition, infected foragers are always assumed to die (there is no recovery from infection), which is realistic given that most parasites known to infect ants require ant death as developmental necessity [406]. For most results we assume that the parasite is constantly present in the environment, though we also explore the potential impacts of seasonality in the force of infection term β , which may arise due to seasonal fluctuations in parasite population size or prevalence. We also formally explore the impacts of changing the parasite-induced mortality rate in Fig. B.3.

3.3.2 Additional model assumptions

Compartments experience identical natural mortality rates.

We assume that ants in all compartments experience an identical rate of natural mortality μ . Empirical estimates of worker mortality rates are scarce in the literature (Table B.4). While we would expect younger ants (brood and nest workers) to have lower natural mortality than foragers, due to their comparative youth and performance of less-risky tasks within the nest, that expectation has not yet been confirmed empirically, nor have the relative mortality rates been quantified. Therefore, we have made the simplifying assumption that all ants have the same lifespan of 1 year, corresponding to a natural mortality rate of $1/365 \text{ days}^{-1}$. We explore the effects of changing the natural mortality rate in Fig. B.2.

No reproductive castes are included.

We do not include any reproductive castes (unmated males (drones), unmated females (gynes), or mated females (queens)) as explicit compartments in our model of mature ant colony dynamics. Reproductives do not follow the same demographic flow (i.e. brood to nest worker to forager) as non-reproductive workers and do not participate in either intranidal or extranidal working tasks [5]. Furthermore, gynes and drones

are expected losses for the colony; they leave on their mating flight and do not return, so whether they become infected once they have left the nest is inconsequential for colony survival (although this does have important consequences for colony fitness). The queen is implicitly included in our model, as she is responsible for the birth of new ants into the brood compartment. However, as she is a singular individual (or a few individuals, in the case of polygynous colonies), we do not create a separate compartment for her.

No seasonality in colony birth rate.

The colony birth rate λ is assumed to depend on the total colony population for which we take into account all model compartments including brood and infected foragers ($F_s + N + B, F_s + F_i + N + B$ for $\beta = 0$ and $\beta > 0$ cases, respectively), but do not take seasonal fluctuations into consideration. Many mature ant colonies fluctuate in their colony sizes and birth rate seasonally [5]. Most of this seasonal fluctuation is due to the seasonal production of reproductive forms; these fluctuations are species-specific and correspond to the synchronous production and release of reproductives for mating flights between colonies. Since we do not include reproductive forms in our model, we do not include seasonality in our birth rate parameter λ , which also has the benefit of rendering our model more analytically tractable.

Only foragers are exposed to ex-nido parasites.

We are investigating parasites infecting ant colonies via an *ex-nido* mode of transmission, which requires extranidal parasite exposure in order to become infected [406]. In many ant societies, this means that only foragers are at risk because only foragers leave the relatively protected confines of the nest. However, some exceptions to this do occur. For nomadic species such as army ants, periodic relocation makes all ants, including brood and reproductives, susceptible to infection, particularly from parasitoids, which can conduct aerial attacks on foraging ants [416]. In other cases, parasites themselves are able to enter the nest independently of the behavior of ant workers, either through mobile stages actively entering the nest (e.g. Syrphid fly microdon larvae) or through parasitoids directly ovipositing their young inside the nest (e.g. some Phorid fly species). For a first attempt at understanding how *ex-nido* parasites impact ant colony dynamics, we have chosen to only focus on the case where foragers are

exposed to parasites. In future work, we hope to address the other ways that *ex-nido* transmitting parasites impact ant colony growth.

No seasonality in the parasite force of infection, β .

For modeling simplicity, we assume that the parasite force of infection term β is constant, though empirical evidence suggests that parasites infecting ants are heterogeneous in both time and space [417, 418]. To assess whether seasonality in the parasite force of infection term might improve colony rescue role, we further investigated how one or two annual peaks in β could impact infection dynamics. To do this, we use standard approaches (e.g. like that used in [419]) and assume that the force of infection term β takes the form $\beta(t) = \beta_0(1 + \beta_1 \sin(2\pi t))$ or $\beta(t) = \beta_0(1 + \beta_1 \sin(4\pi t))$, where t is in years but is adjusted to match our time scale, to get one or two annual peaks, respectively. We explore the impacts of seasonality in Figs. 3.6, B.5, B.6.

Model parameters

A description of the model parameters and their values are given in Table 3.1. Whenever possible, estimates of model parameters were extracted from published values. We provide a detailed discussion of how model parameter values were chosen and summarize empirical estimates from the literature in Appendix B and the tables therein.

3.4 Results

We are ultimately interested in the impact of *ex-nido* parasitism on ant colony dynamics under biologically realistic parameter space. To that end, here we first provide validation of our model in the absence of parasitism, and then show how our model predicts parasite-induced impacts on colony dynamics under changing values of colony birth rate and parasite force of infection. Finally, we assess model sensitivity to different parameter values such as changing the proportion of the colony foraging, changing the natural mortality rate, and adding seasonality to the parasite force of infection.

3.4.1 Baseline model validation

To understand the effect of *ex-nido* parasitism on ant colony dynamics we first examined dynamics in the absence of parasitism (force of infection $\beta = 0 \text{ days}^{-1}$), using baseline parameter values given in Table 3.1. Using linear stability analysis and confirmation via direct numerical simulation, we found that for all birth rates in the range of modeled values, colony growth reaches equilibrium in approximately 1,500 days, which corresponds well to knowledge of ant colony development from inception to colony maturity [5, 58, 88, 420, 421]. To assess how the model reacts to population perturbations in the absence of *ex-nido* parasitism, we simulated the removal of a fixed percentage of each compartment (B, N, F_s) after equilibrium had been reached (Fig. B.1). In all cases, as long as the population had not been reduced below the minimum value necessary to sustain colony functioning (σ , Table 3.1), each compartment was able to recover back to their equilibrium values. The time it took to recover from the perturbation to 90% of equilibrium values was 600 - 820 days (2 - 3 years) and 1,110 - 1,650 days to return to full equilibrium values. While it is unknown how long it would take an ant colony to recover back to pre-perturbation population values in a natural setting, it seems realistic that the recovery period is on par with the growth period of an incipient ant colony reaching maturity.

3.4.2 Equilibrium values and bifurcation diagrams

The equilibrium values for each compartment within the uninfected model ($\beta = 0 \text{ days}^{-1}$) under baseline parameter values (Table 3.1) are as follows- F_s : 1,045.91 ants, N: 2,118.56 ants, and B: 485.507 ants, which is a realistic colony size for many ant species [5, 89]. The equilibrium values for each compartment within the infected model ($\beta = 0.01 \text{ days}^{-1}$) under baseline parameter values (Table 3.1) are F_s : 458.134 ants, F_i : 31.4659 ants, N: 1,034.09 ants, and B: 485.499 ants. Bifurcation diagrams for the model when $\beta = 0$ (uninfected) and when $\beta > 0$ (infected) are provided in Figs. 3.3a and 3.3b, respectively. In Fig. 3.3a, the bifurcation diagram switches from a stable to unstable regime at the minimum colony size needed for functioning ($\min = 10$ ants). In Fig. 3.3b, the bifurcation diagram with respect to β remains stable throughout the range of β values for a colony birth rate $\lambda = 10$ ants/day.

3.4.3 Changing birth rate, λ , and force of infection, β

We next examined colony dynamics in the presence of *ex-nido* parasitism. Under the baseline colony birth rate and force of infection given in Table 3.1, we observe an equilibrium reduction of 45.8% in colony size in the infected model relative to the uninfected model (i.e. $\beta = 0 \text{ days}^{-1}$). It takes approximately 2,900 days to reach this full equilibrium reduction and approximately 800 days to be within 10% of equilibrium values. When β is fixed at the baseline value of $\beta = 0.01 \text{ days}^{-1}$ and we assume different values of colony birth rate λ from 1 - 100 brood/day, we predict that the proportion reduction in colony size remains essentially the same (Fig. 3.4a), and it takes 700 - 900 days to be within 10% of equilibrium values. When we fix colony birth rate λ at the baseline value of $\lambda = 10 \text{ brood/day}$, chosen because it's in the middle of log scale realistic values for colony birth rates (see Table B.1) and traverse values of β in the range of $\beta = 0.0001$ to 1 day^{-1} , we find a wide range in resulting proportion reductions in colony size, from 1% up to 77%, respectively (Fig. 3.4a). This is realistic because β controls the rate at which foragers are lost due to parasitism; above a certain value of β the colony's birth rate can no longer compensate for the loss of foragers and thus larger reductions in colony size occur (Fig. 3.4).

3.4.4 Impact of the proportion of the colony foraging, κ

The proportion of the colony that forages κ is an important model parameter because it impacts the number of individuals in the susceptible forager F_s compartment and thus the number of individuals at risk of becoming infected. Altering the proportion of the colony foraging κ had a large impact on the resulting percent reduction in colony size relative to the uninfected model (Fig. 3.5a) and on the total colony size at equilibrium (Fig. 3.5b). When 10% of the colony forages under baseline model conditions, there is a 22.8% reduction in colony size compared to the uninfected model; in contrast, when 70% of the colony forages, there is a 61.3% reduction in total colony size relative to the uninfected model (Fig. 3.5a). This translates into a large difference in resulting total colony sizes for a typical ant colony: 2,816 ants vs. 1,412 ants, for $\kappa = 0.10$ vs. 0.70 , respectively. By allowing a larger proportion of the colony to be in the susceptible forager (F_s) compartment, more individuals are at risk for becoming infected, and so a larger number of individuals die due to parasite-induced mortality rather than natural mortality. Our model, which makes

the simplifying assumption that foragers experience the same natural mortality as their non-foraging counterparts, likely overestimates the percent relative reduction in colony size between infected and uninfected models because foragers likely do experience a higher rate of natural mortality.

3.4.5 Adding seasonality to parasite transmission rate

To assess how seasonality in the parasite force of infection term β could impact colony dynamics, we simulated outbreaks in which β varies over time rather than being held at a fixed value. To accomplish this, in these simulations the force of infection term β takes the form $\beta(t) = \beta_0(1 + \beta_1 \sin(2\pi t))$ or $\beta(t) = \beta_0(1 + \beta_1 \sin(4\pi t))$, to get one or two seasonal peaks per year, respectively. We plot these seasonally varying values of β and their impacts on the percent colony reduction relative to the uninfected model in Figs. B.5, B.6 and we show a comparison of model predictions for total colony size in cases where β is either constant, has 1 seasonal peak per year, or has two seasonal peaks per year in Fig. 3.6. When β reaches a seasonal peak, colony sizes in all three cases approximately mirror each other. However, including seasonality in the force of infection term β allows colony size to rebound slightly, resulting in a higher average colony size over time Fig. 3.6. Thus, our results in Fig. 3.4a, in which parasitism is assumed to be constant, represent the ‘worst-case’ scenario for a given value of β .

3.4.6 Changing the natural mortality rate μ

As the natural mortality rate decreases (i.e. individuals live longer), the total population increases markedly (Fig. B.2b). When *ex-nido* parasites are present ($\beta > 0$), changing the natural mortality rate can also cause large differences in the percent reduction in total colony size between the infected and uninfected models (Fig. B.2a). For example, when we take an average ant lifespan of 1 year ($\mu = 1/365 \text{ days}^{-1}$), which has been reported for worker ants, the percent relative reduction in total colony size is approximately 44%, whereas when the average lifespan is assumed to be 30.4 days ($\mu = 1/30.4 \text{ days}^{-1}$), the percent relative reduction is approximately 3%. An average longer lifespan increases the relative impact of parasitism on the colony in two ways. Firstly, foragers live longer and thus have more cumulative exposure to parasites over the course of their longer lifespan, resulting in a larger number of infected foragers at equilibrium. Secondly, as the lifespan of individuals increases, there is a larger

disparity between the parasite-induced mortality rate γ and the natural mortality rate μ , resulting in a larger disparity when comparing the colony population sizes of the infected and uninfected models. In the uninfected model, fewer individuals are dying due to natural mortality, so there is a larger population size, while population loss in the infected model is being driven primarily by parasite-induced mortality.

3.4.7 Changing parasite-induced mortality rate, γ

Changing γ , the parasite-induced mortality rate for infected foragers, alters the equilibrium number of infected foragers. In our model, infected foragers are assumed to behave as healthy foragers, don't infect others, and are considered part of the total population size that is used to calculate the fraction of the colony that is foraging. Thus, when the parasite-induced mortality γ is lower (but still faster than the rate of death due to natural mortality), infected foragers survive longer and replacements do not need to be recruited from the nest worker population as frequently, which helps reduce the size of the forager population that is exposed to infection at rate β . However, this difference has only a small impact on the percent reduction in colony size relative to the uninfected model (Fig. B.3a) and the total colony size at equilibrium (Fig. B.3b). When γ is $1/30 \text{ days}^{-1}$, the resulting percent population reduction is 43.3%, while the percent reduction only increases slightly to 46.6% when γ is changed to 1 days^{-1} (Fig. B.3a). Thus, model outcomes are not very sensitive to changes in γ within biologically reasonable ranges.

3.4.8 Conditions for colony collapse

Given specific colony parameters, we can use our model to predict colony size reduction or collapse. In the case of the baseline parameters (Table 3.1), colonies are vulnerable to collapse when the birth rate λ is less than 0.2328 ants/day, which we calculate via linear stability analysis of Eqs. (1 - 4) in the limiting case of $\beta \rightarrow \infty$. That is, if λ is above this threshold then collapse will not occur, though the extent of colony size reduction will depend on the strength of the force of infection β (Fig. 3.4a,b). In Fig. 3.4b, the only value of λ that results in collapse is less than this threshold, and in Fig. 3.4a, the upper boundary of the collapse region asymptotically approaches this value. If λ is less than the threshold value of 0.2328 ants/day, the colony may collapse if β is sufficiently large. Though the total colony size at equilibrium is sensitive to

changing values of κ , the birth rate threshold above which collapse will not occur is not sensitive to changing values of κ . For example, for $\kappa = 0.01$, the minimum value of λ is 0.0656 brood/day, whereas for $\kappa = 0.5$, the minimum value of λ to avoid collapse is 0.2736 ants/day. While ant colony birth rates are species-specific and likely do vary seasonally, a birth rate of 0.2328 ants/day is much lower than those reported in the literature (Table B.1). For much of the parameter space explored in our model (Fig. 3.4a), colony collapse is not predicted to occur.

3.5 Discussion

The ants and other social insects are complex societies that have evolved over long periods of evolutionary time [38]. For the ants we know this to be between 139 - 158 million years, which parallels major changes in ecological complexity, such as the radiation of the angiosperms and expansion of other insect groups [30]. During this time period, ants evolved to be the dominant animals in most terrestrial biomes; despite accounting for 0.4% of the estimated 5.5 million insect species [422], they typically comprise > 50% of animal biomass [10,61]. This success seems paradoxical, as ants are host to diverse parasites [22, 91, 406] and seem to be particularly vulnerable to infectious disease outbreaks due to living in crowded conditions with lots of highly related individuals. Accordingly, a lot of research has been devoted to uncovering potential mechanisms by which ants and other social insects might mitigate potential disease spread inside their colonies (reviewed in [91, 97, 99, 129]). However, the majority of the parasites that infect ants and social insects use lifecycles that preclude intra-colony transmission, instead requiring periods of time outside the nest for development in the environment or in other hosts before the next transmission event to ants can occur [91, 406]. The impact of these parasites on colony dynamics has been hitherto unexplored.

Here we formally explored the potential for epidemic collapse due to these *ex-nido* parasites by modeling the impact of their infection on ant colony dynamics. Using parameter values extracted from the literature (Appendix B), we found that in the absence of parasitism, colonies can recover from population perturbations back to equilibrium values within approximately 1,100 - 1,650 days (Fig. B.1), which is in general accord with reported growth rates of colonies as they mature [420]. Such perturbations might reflect attack by predators or competition with other colonies.

We then modeled the presence of *ex-nido* parasites and showed that for a wide range of biologically plausible birth rates the effect of parasitism ranged from negligible impacts on colony population (< 10% colony size reduction, Fig. 3.3a) to significant reductions (>90% colony size reduction, Fig. 3.3a), depending on the magnitude of the force of infection parameter β . Under the baseline parameters used in our model, colonies are not vulnerable to parasite-induced collapse unless λ is below 0.2328 ants/day, which is much lower than birth rates reported in the literature (Table B.1). Thus our modeling predicts that under realistic parameter values, infection by *ex-nido* parasites will not result in colony collapse.

An important question is whether values of β large enough to cause collapse could be achieved. A key result of this study is that the impact of *ex-nido* parasitism depends most heavily on the force of infection β , a parameter that combines the frequency with which foragers are in the extranidal environment, how frequently foragers encounter parasites while in that environment, and the probability of successful infection given contact with a parasite. While few if any empirical estimates of the components of β are known (see additional discussion in Appendix B), if foragers make trips very often, encounter parasites very frequently, and/or are unable to prevent successful infection by behavioral, social, or physiological immune mechanisms, then such values could indeed occur. The little information we do have on the individual components of β suggests that the parasite infective pressure that ants face is probably quite heterogeneous in both time and space [231, 423, 424]. For modeling simplicity we have assumed, for our main results, that parasite pressure is constant, but many parasites of social insects undergo seasonal fluctuations in their populations [418, 425, 426]. When we investigated seasonality by allowing for one or two annual peaks in parasite force of infection β , colonies were able to rebound and colony size were slightly larger on average (Fig. 3.6). Our model, which assumes a constant rate of parasite infection, therefore represents an upper bound to the impact of *ex-nido* parasite pressure on ant colony size. Additionally, we know that ants are able to behaviorally mitigate their potential exposure to parasites by reducing foraging [427–429] and can prevent exposure from developing into infection via self- and allogrooming behaviors [139, 140]. Our model, which does not include behavioral flexibility or behavioral anti-parasite defenses, likely overestimates the impact of parasitism. Thus, the conditions that lead to model-predicted colony collapse provide a worst-case scenario for the colony, and these conditions are unlikely to occur in natural settings.

Furthermore, the timing over which these parasite-induced colony size reductions occur plays an important role in colony robustness; these reductions take place over years, not in a matter of days (approximately 800 days or over 2 years to be within 10% of full equilibrium reduction under baseline parameters), causing a gradual thinning of colony size. This contrasts with what we observe in high density, group living mammals where a sudden catastrophic loss of individuals can occur, like that recently observed during the Saiga antelope epizootic [430] or occurring in tropical forest mammal populations due to anthrax [431]. In natural settings, ant colonies might be able to adapt to or mitigate this gradual parasite-induced loss of workers before collapse occurs, through changing behavioral defenses [427], moving nest locations [432], or potentially increasing birth rate in compensation.

What happens in cases where colony size is reduced by parasitism but collapse does not occur? Few studies have explored the impact of parasite-induced colony size reduction on colony functioning, organization, or fitness. Ants and other social insect colonies do have built-in redundancy to buffer loss [5, 50, 58]. Schmid-Hempel and Heeb [433] found that imposing an extra 10-15% weekly mortality rate on *Bombus lucorum* colonies did not alter colony growth rate or reproductive output compared to control colonies. Follow-up work by Müller and Schmid-Hempel [434] experimentally removed 10% of the worker force each day in *B. lucorum* colonies and found no difference in worker production or the timing of reproduction but there were reductions in either the number of males produced or female reproductive body size depending on when worker loss occurred. One proxy for forager loss may be circumstances where foragers do not leave the colony for resources because of risk of death from abiotic factors like heat. In a long term study on the desert foraging ant *Pogonomyrmex barbatus*, Gordon [435] showed that colonies could reduce the number of foraging trips to avoid worker desiccation and still achieve colony growth and colony fitness (number of daughter colonies produced).

Are there any examples of parasites causing epidemic colony collapse in natural populations? For the ants, to our knowledge there are no reports of parasite-induced colony collapse for mature colonies, but there are examples of colonies persisting despite the multi-year presence of *ex-nido* transmitting parasites [231]. While attempts to use both *in-nido* and *ex-nido* transmitting parasites as biocontrol agents against pestiferous ant species have been numerous (see review by [436]), their lack of success highlights how difficult it is to perturb a mature ant colony to collapse [232, 437, 438].

Parasite pressure is most certainly a significant selective pressure on incipient colonies [5], however; this is extremely hard to observe in field settings and so associated data is extremely limited.

Some social insects are famously experiencing collapse. Managed bee colonies and global bee populations have been experiencing significant decline beginning in the early 2000's [439, 440], but it appears that a constellation of causes including pesticide usage, habitat loss, chronic stress, and directly transmitting parasites coupled with ectoparasites (mites) contributed synergistically to the reported losses [441]. Our understanding of the parasite pressure that social insect colonies face in nature remains limited, but it seems that parasite-induced collapsed of mature social insect colonies in natural populations are rare events, and our model suggests that parasite-induced collapse by *ex-nido* transmitting parasites would take years, not days or months, to occur.

What makes ant and other social insect colonies so resilient in the face of possible disease threats? Unlike other animal societies and group living organisms, ants and social insect colonies employ an efficient division of labor that allows for the loss of individuals while maintaining colony functioning [5, 50, 58]. Furthermore, it is this very division of labor that helps mitigate disease exposure by limiting the number of individuals who leave the protected confines of their nest, a form of 'organizational immunity' [129]. Finally, strong physiological and social immune defenses inside the nest help prevent the potential onward transmission of directly transmitting parasites (reviewed in [91, 97, 99, 127, 129]).

3.6 Conclusions

Ants and other social insects have had to contend with the intense selective pressure imposed by parasites and pathogens over their long evolutionary history. The ability to prevent outbreaks likely reflects early selection prior to their transition to a eusocial lifestyle [92]. This is especially important for the ants, which evolved colony life from a starting position in microbe rich soils [90], likely necessitating possessing a strong prophylactic disease defense system. Work has shown that ants and social insects do have an impressive suite of behavioral and physiological immune mechanisms at their disposal [91, 97, 99, 127, 129]. The evolution of a eusocial lifestyle, in which fitness lies at the level of the colony and not at the level of the individual, coupled with

these strong anti-parasite defenses and lots of evolutionary time, has likely facilitated the co-evolution of *ex-nido* transmission strategies on the part of their parasites [47], which remains an exciting and underexplored area of research. Our work here shows that parasites that require leaving the nest before the next transmission event to ants can occur are likely to have a limited impact on mature colony dynamics, precluding epidemic collapse. This then may be a key difference between social insect societies and other animal societies, where massive outbreaks of infectious diseases are routine and destabilizing to group functioning.

Acknowledgments

We would like to thank Timothy C. Reluga for technical guidance in modeling analysis and for insightful discussions thereof. We would also like to thank members of Penn State's Center for Infectious Disease Dynamics for helpful comments and feedback on this work. Finally, we gratefully acknowledge the many natural historians who have collected records of parasites infecting ants as well as the myrmecologists who have studied ant life history traits. Their work provides the biological foundation on which this and other studies can be built.

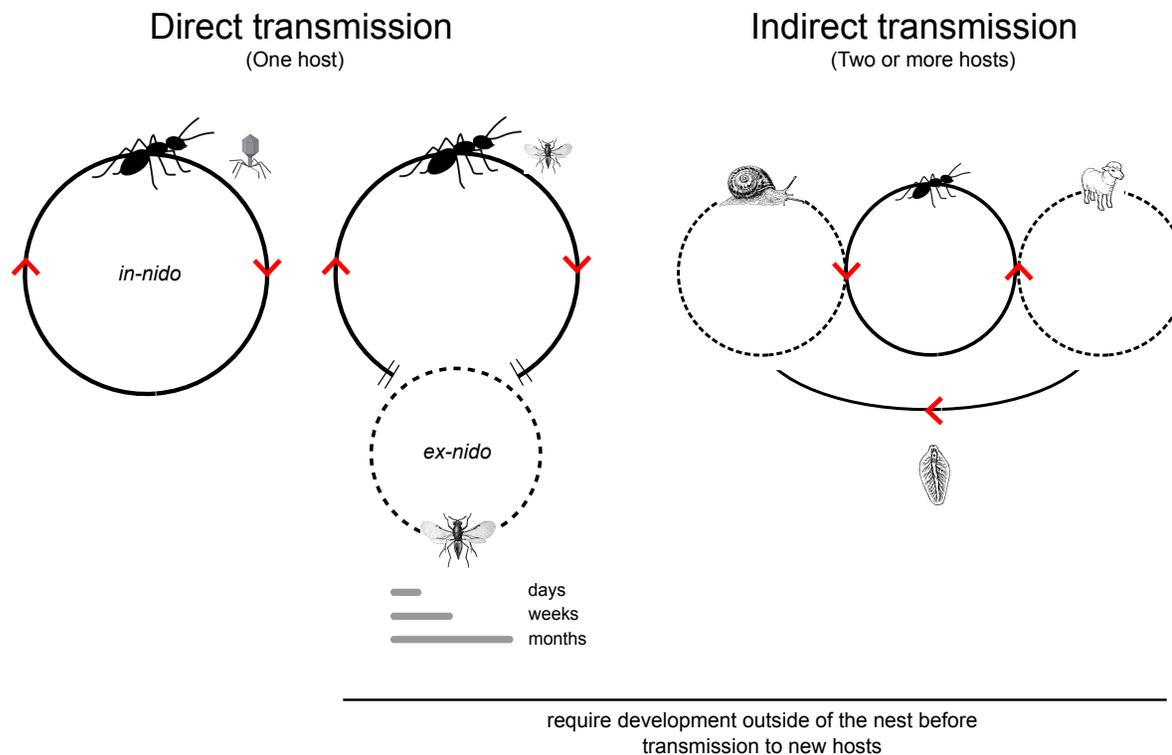
3.7 Figures and Tables

Table 3.1: Model parameters.

Description of model parameters, the range of their values, and the baseline values used in the modeling analysis.

Model parameters				
Parameter	Unit	Definition	Modeling range	Baseline value
Lambda, λ	ants/day	Colony birth rate	1 - 100	10
Phi, ϕ	days ⁻¹	Brood - nest worker transition rate	-	1/56
Alpha, α	days ⁻¹	Nest worker - forager transition rate	0.1 - 1	0.1
Kappa, κ	-	Max proportion of the colony in the forager compartment	0.1 - 1.0	0.3
Sigma, σ	ants	Minimum colony size	-	10
Mu, μ	days ⁻¹	Natural mortality rate	1/760 - 1/30	1/365
Beta, β	days ⁻¹	Per-capita parasite transmission rate	0.0001 - 1	0.01
Gamma, γ	days ⁻¹	Parasite-induced mortality rate	1/30 - 1	1/7

Figure 3.1: Transmission strategies used by parasites infecting ants.



(a) Direct, *in-nido* parasitism occurs when ants are the only host infected and transmission can readily occur from ant-to-ant inside the nest. Examples include bacteria, viruses, and some entomopathogenic fungi. (b) Direct, *ex-nido* parasitism occurs when ants are the only host infected, but the parasite needs to complete development in the extranidal environment before it is capable of transmitting to the next ant host. Examples include parasitoid wasps and flies. (c) Indirect, *ex-nido* transmission occurs when more than one host species is required for the parasite to complete its lifecycle. The use of multiple hosts necessitates development outside of the nest. Examples include cestode, trematode, and some nematode worms.

Figure 3.2: Schema for the model of colony growth in the absence and presence of *ex-nido parasitism*.

Model compartments and flow. Brood (B) are born into the colony according to birth rate λ . Brood transition to become nest workers (N) according to the developmental rate, ϕ . Nest workers transition to become susceptible foragers (F_s) according to colony need (κ) by rate α . Finally, susceptible foragers can become infected (F_i) according to the parasite force of infection term, β . All compartments experience the same natural mortality rate, μ .

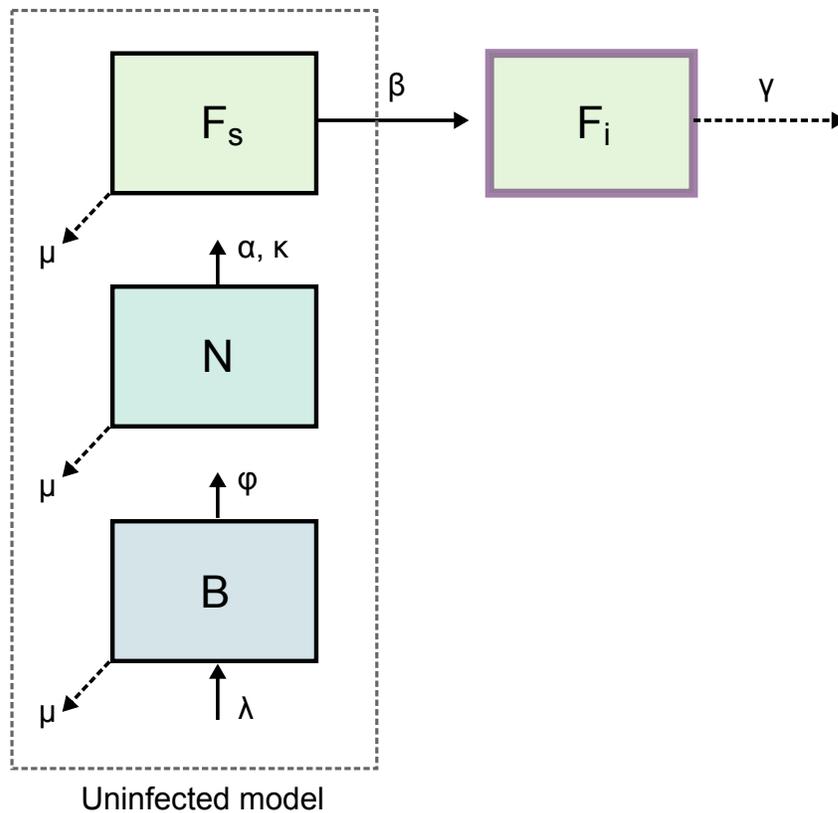
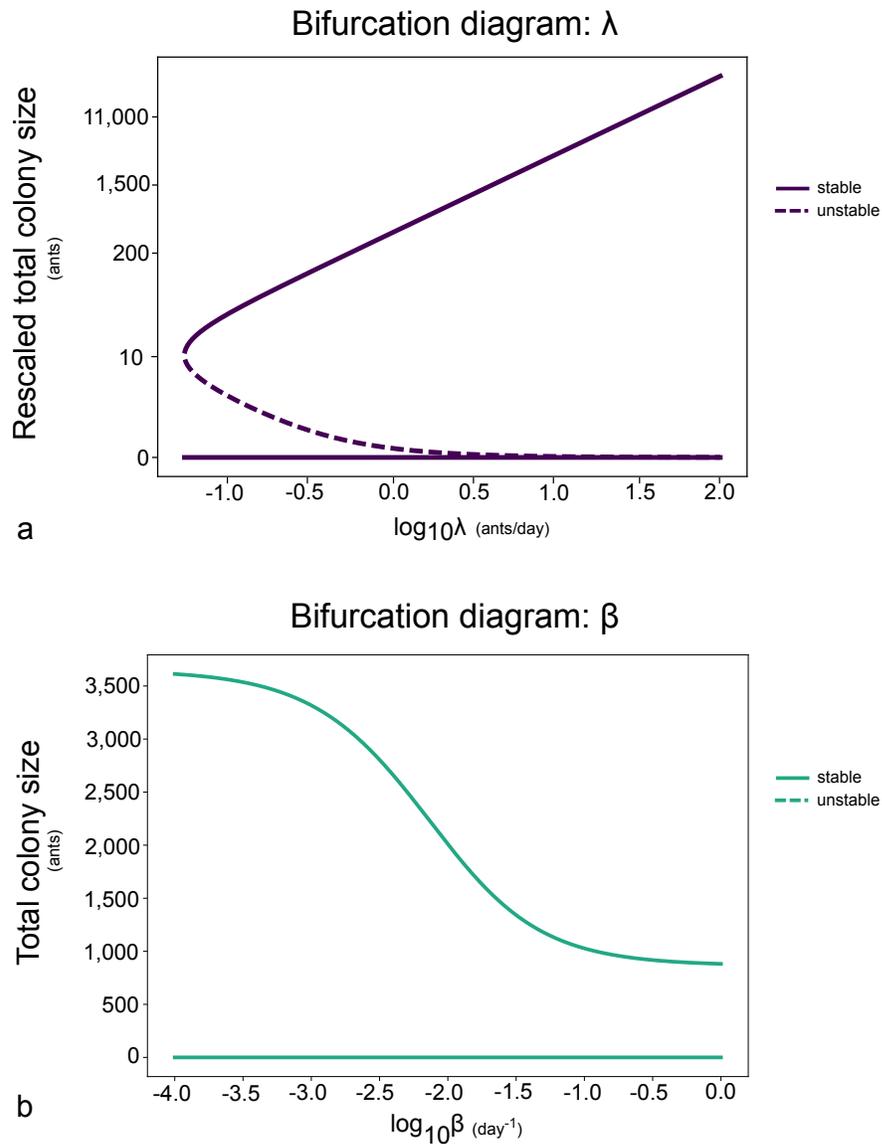
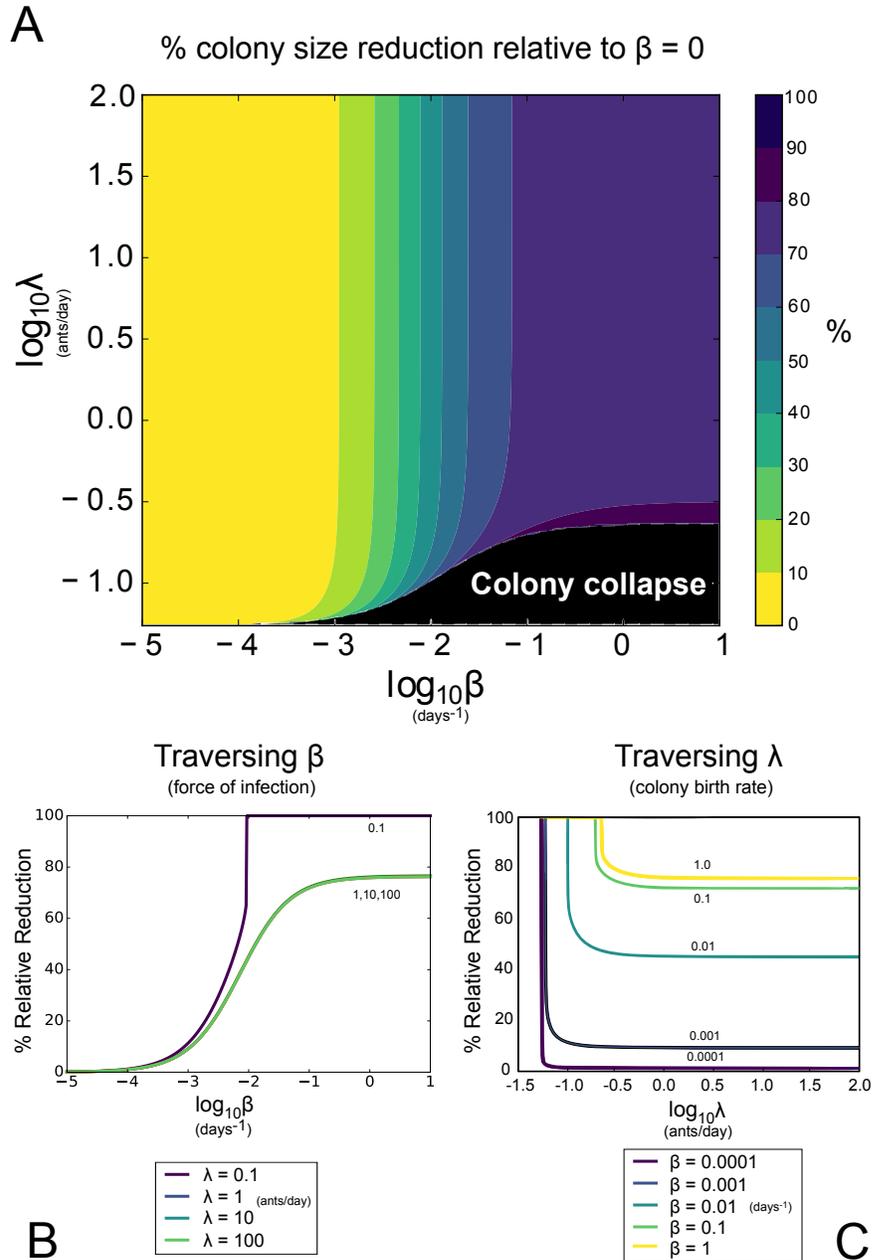


Figure 3.3: Bifurcation diagrams with respect to colony birth rate λ and parasite force of infection, β .



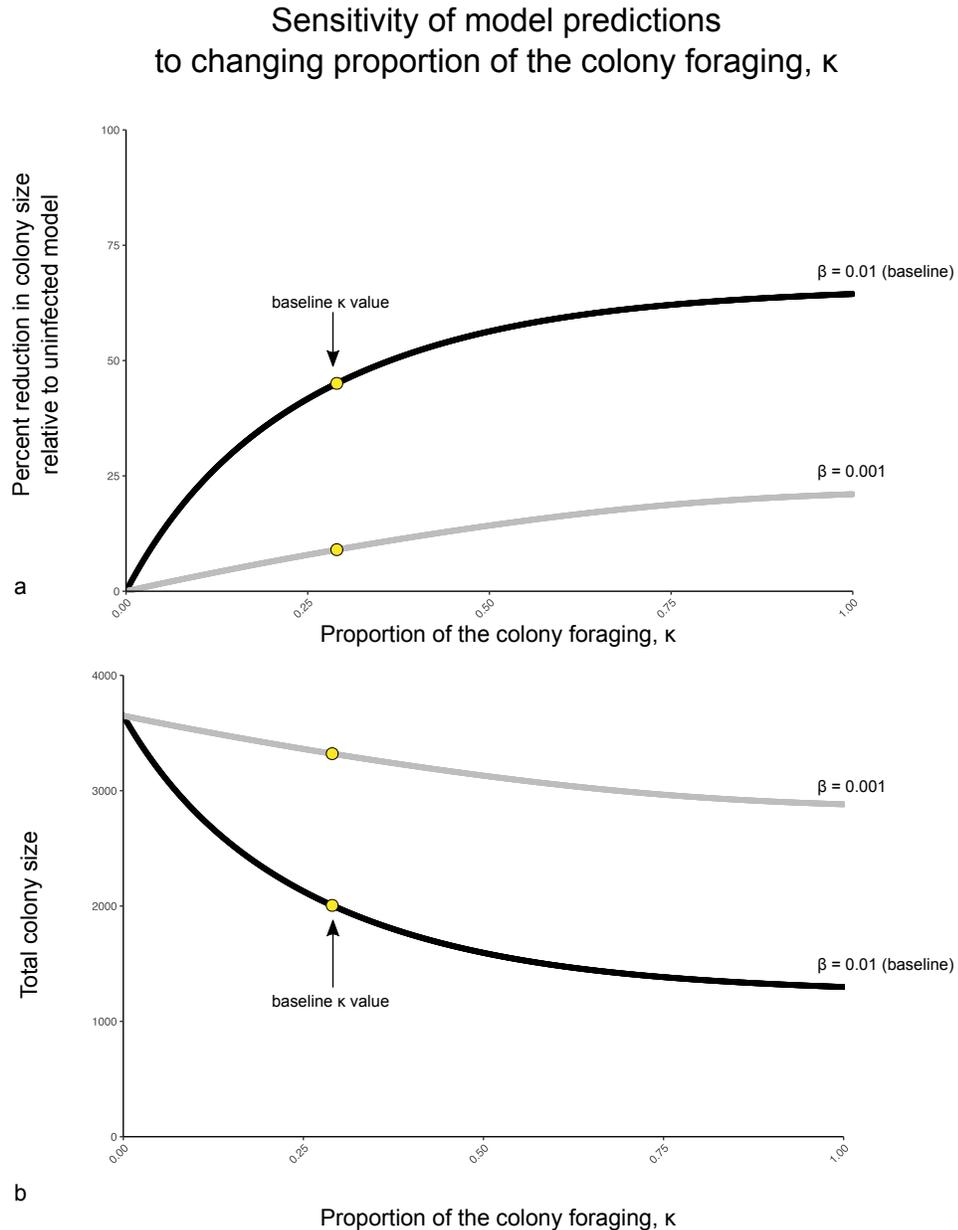
(a) Bifurcation diagram for the uninfected model (eqs. 1-3, $\beta = 0$) under baseline parameter values given in Table 1. Rescaled colony size as a function of colony birth rate. Colony size was rescaled using an arcsinh function. (b) Bifurcation diagram for the infected model (eqs. 1-4) under baseline parameter values given in Table 3.1.

Figure 3.4: Modeling the impact of *ex-nido* parasitism on colony growth dynamics.



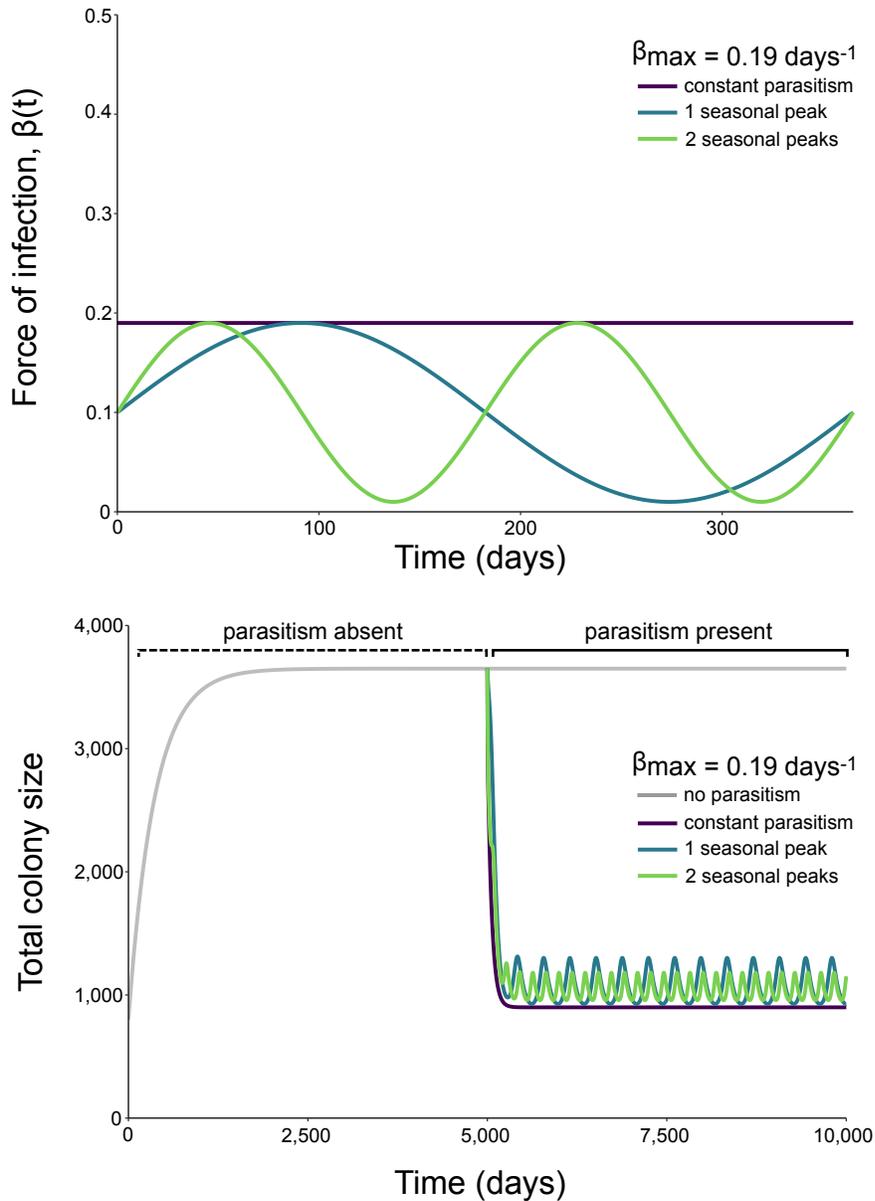
(a) Contours in percent reduction in colony size predicted by our model (Eqs. (1-4)) as a function of colony birth rate λ and force of infection β relative to when $\beta = 0$. Other parameters can be found under baseline values in Table 3.1. (b) Percent reduction in colony size predicted by our model (Eqs. (1-4)) as a function of rate of infection β and $\lambda = 10$ brood/day relative to when $\beta = 0$. Other parameters can be found under baseline values in Table 3.1. (c) Percent reduction in colony size predicted by our model (Eqs. (1-4)) as a function of colony birth rate λ and $\beta = 0.01$ relative to when $\beta = 0$. Other parameters can be found under baseline values in Table 3.1.

Figure 3.5: Sensitivity of model predictions to changing the proportion of the colony foraging, κ .



Model predictions are from numerical simulation under baseline parameter values given in Table 3.1. (a) The proportion reduction in colony size relative to the uninfected model under changing values of κ from 0 to 1. (b) Total colony size ($F_s + N + B$) under changing values of κ from 0 to 1.

Figure 3.6: Comparing the impact of constant vs. seasonal parasitism.



(a) Values of the force of infection term β under constant and seasonal parasitism with one or two peaks. The maximum values of $\beta = 0.19 \text{ days}^{-1}$. (b) Model predictions of colony size when there is no parasitism present, parasitism is present under baseline values that are constant, parasitism fluctuates seasonally with one annual peak, or parasitism fluctuates seasonally with two annual peaks. Model predictions are from numerical simulation under baseline parameter values given in Table 3.1 and $\beta = 0.19 \text{ days}^{-1}$.

**Corpse management and behavioral avoidance
reduce the potential of epidemic disease spread in
ant colonies**

4.1 Abstract

Ant colonies have likely been subject to intense selective pressure from parasitic organisms over their long evolutionary history. As such, the ants possess many anti-parasite defenses to prevent epidemic collapse within their colonies. Among these, empirical work has shown that behavioral defenses are important for reducing the spread of disease between nest mates. We add to this knowledge through a theoretical framework by creating a stochastic SIR-type compartmental model of within-colony disease spread to assess the importance of two of these defenses, behavioral avoidance and corpse management, on mitigating epidemic outcomes. We find that both behavioral defenses can reduce the potential of catastrophic epidemic spread, and their use may explain the lack of observations of mature ant colony collapse in natural settings.

4.2 Introduction

The transition to group living is an evolutionary achievement that has facilitated the development of many beneficial traits [31]. Despite these benefits, increased disease transmission is a significant cost of sociality, with parasite levels generally assumed to increase with host group size [2, 3, 74, 77, 96] (cf. [87]). Dense living

conditions, increased contact with potentially infectious individuals, and the buildup of environmental fomite all contribute to the generally positive relationship between group size and parasite abundance.

Ants (Hymenoptera: Formicidae) exemplify the living conditions that exaggerate the risk of intra-colony infectious disease spread, living in large colonies [89] (reviewed in [88]) with nesting habitats that often put them in increased contact with microbial loads. Ants are known hosts to over fifty different parasite families [91, 406], ranging from viral and fungal pathogens to helminth and insect parasitoids (hereafter, collectively referred to as ‘parasites’). These diverse taxa have likely imposed a high selective pressure on the ants over their long evolutionary history [92].

In spite of this, ants are one of the most ecologically dominant organisms on Earth [5, 6], suggesting that they have been successful at buffering the negative effects of infectious disease. Indeed, it is likely that many mechanisms of anti-parasite defense were necessary for the transition to permanent group living to occur [78, 92]. Empirical work over the past two decades has been dedicated to uncovering the mechanisms that could mitigate disease spread within colonies [132, 140, 409, 442–444]. Together, this body of work (reviewed in [91, 97, 99, 127, 129]) has revealed many ways through which the disease-related costs of sociality might be offset.

A key generalization from this work and those in other animal systems is that behavioral defenses, both prophylactic and inducible, can play a significant role in preventing epidemic outcomes [96, 445–448]. Behavioral defenses used by ants and other social insects can be nuanced and complex. They include the spatial organization of colonies to prevent contact between potentially infected individuals [152, 449] (reviewed in [129]), and limiting movement around infectious pathogens (E. Solá Gracia, personal communication). Defenses can also be actively employed, such as grooming to remove infectious material [133], forcibly removing infected nest mates [60, 146], sanitizing nest material and nest mates [450], or effectively managing corpses (necrophoresis) within the nest (reviewed in [147, 444]).

While it is preferable to prevent parasites from entering the nest in the first place, once parasites have entered, the management of corpses and other potentially infectious waste becomes a particularly important behavioral defense [147]. Disinfection and removal behaviors have been studied across social insect taxa [150, 151, 451, 452], as has the potential for disease outbreaks in sub-colonies [438, 453], but few studies have explicitly correlated necrophoric behaviors with resulting disease outcomes

[146, 454, 455]. Chouvenc and Su (2012) showed that when exposed to *Metarhizium anisopliae* infected individuals, *Coptotermes* individuals were able to prevent epizootics through the cannibalism, burying, and physical segregation of infectious corpses [454]. Diez et al. (2015) observed similar results in colonies of *Myrmica rubra* exposed to *Metarhizium* infected corpses; though individuals in exposed colonies had higher mortality rates than control treatments, epidemic spread was prevented and correlated with an increase in hygienic behaviors [455]. Pull et al. (2018) showed that *Lasius neglectus* ants could discriminate infected but not yet infectious pupae and destroy them by spraying acid, preventing epidemics before they even started [146].

As a complement to these empirical studies, here we employ a theoretical model to explore the effects of corpse management (e.g. removal or disinfection) and social segregation (i.e. reduced contact rates between colony members and infectious corpses) on the potential for ant colony epidemic collapse. Using the pathogens *Metarhizium sp.* and *Beauveria sp.*, as models, we build a stochastic compartmental ‘SIR’-type model of disease transmission within age-structured ant colonies. We first assess colony performance in the absence of disease to validate the model, and then we introduce *in-nido* parasitism to see what the consequences of unmitigated infection are on potential for colony collapse. We next explore how modulating cadaver contact rate (social segregation) and cadaver decay rate (corpse management) impact predictions for colony collapse. We find that both behavioral defenses can reduce the potential for disease-induced colony collapse, and their use may explain the lack of observations of mature ant colony collapse in natural settings.

4.3 Methods

Model of ant colony dynamics in the presence and absence of *in-nido* transmitting parasites

We base our model of mature ant colony dynamics in the absence of parasitism on that given in Chapter 3, eqs. 3.1 - 3.3. Below we describe our model of ant colony dynamics in the presence of *in-nido* parasites, our model assumptions, and summarize the model schematically in Fig. 4.1.

Ants are assumed to transition through three compartments that correspond to ant developmental and sociological castes: brood (**B**), nest worker (**N**), and forager (**F**).

Our model adds in an additional compartment for the queen (**Q**), who is particularly important because colony fitness depends on her reproductive success over the course of the colony's lifetime.

Infections are initially brought into the colony by foraging ants **F**, who come into contact with infectious spores in the extranidal environment according to the parasite force of infection term β . Following exposure, these foragers become infected, **I**, but are not yet infectious because parasite development requires the death of the host before the next host can become infected. Infected foragers **I** die with parasite-induced mortality rate γ to become infectious cadavers, **C**. Infectious cadavers decay over time, according to the cadaver decay rate ζ . Once infectious cadavers are present in the colony, we assume that all compartments (**F**, **N**, **B**, **Q**) can become infected through contact with these cadavers, with compartment-specific contact rates $\psi_F, \psi_N, \psi_B, \psi_Q$. All infected ants, regardless of what compartment they originate from, transition into the same infected ant compartment **I** and then into the cadaver compartment **C**. The equations below represent the deterministic version of the model and they approximate mean behavior for the stochastic implementation of the model:

$$\frac{dB}{dt} = \frac{\lambda(F + N + B)^2}{\sigma^2 \left(1 + \frac{(F+N+B)^2}{\sigma^2}\right)} - \phi B - \mu B - \psi_B B \quad (4.1)$$

$$\frac{dN}{dt} = \phi B - \alpha N \left(\kappa - \frac{F}{1 + F + N + B} \right) - \mu N - \psi_N N \quad (4.2)$$

$$\frac{dF}{dt} = \alpha N \left(\kappa - \frac{F}{1 + F + N + B} \right) - \mu F - \beta F - \psi_F F \quad (4.3)$$

$$\frac{dQ}{dt} = -\mu_Q - \psi_Q \quad (4.4)$$

$$\frac{dI}{dt} = \beta F + (\psi_B B + \psi_N N + \psi_F F) C - \mu I - \gamma I \quad (4.5)$$

$$\frac{dC}{dt} = \gamma I - \zeta C \quad (4.6)$$

Model assumptions

Please refer to Chapter 3 and Appendix B for a discussion of model assumptions relating to ant colony demography. We assume that all workers (**F**, **N**, **B**) have the same natural mortality rate, μ and the queen (**Q**) has a longer life span and thus lower natural mortality rate, μ_Q . We make the simplifying assumption that infected ants (**I**)

behave in all respects like their uninfected nest mates.

Model parameters

Model parameter baseline values and modeling ranges are given in Table 4.1. A discussion of model parameter choice as well as reported parameter values from the literature are provided in Chapter 3 and Appendix B for parameters related to ant colony demography. For the parameters related to the fungal infection we model here, such as cadaver contact rates ($\psi_F, \psi_N, \psi_B, \psi_Q$) and cadaver decay rate ζ , few empirical estimates have been published. We base our modeling ranges on those reported in unpublished empirical work (E. Solá Gracia).

Model simulations

We implement stochasticity into our model using the Gillespie direct method [456]. In the Gillespie direct method, the rates of all model transitions are summed together to determine the time to the next event, and the next event that occurs is a random draw conditional upon the relative rates in the model.

Simulations were run in R [457] using bespoke code (Appendix C). For each parameter set, 1,000 simulations were run, with a maximum number of time-steps per simulation set to 30,000. Simulations were halted under three conditions: the queen died (resulting in colony collapse), the total colony size was less than the minimum number needed for colony functioning ($\sigma = 10$, resulting in colony collapse), or the maximum number of simulation time steps had been reached. For each simulation, we recorded the maximum time (days) reached and the number of individuals in each compartment at that maximum time.

4.4 Results

In this work, we are interested in assessing how the presence of *in-nido* transmitting parasites impacts colony dynamics, and whether social segregation from infectious cadavers or increased cadaver decay rates due to corpse management could impact epidemic outcomes. Below we describe model predictions in the absence of parasitism, in the presence of parasitism without behavioral immune mechanisms, and in the

presence of parasitism with behavioral immune mechanisms. Please note that these results are preliminary; more simulations need to be run for each parameter set.

Model validation in the absence of *in-nido* parasitism

In the absence of *in-nido* parasitism, the model simplifies to the uninfected model form given in Chapter 3, with the additional inclusion of the queen compartment. We confirmed the stochastic implementation of this model under the baseline model parameters given in Table 4.1, which are identical to the baseline model parameters used in Chapter 3 (Table 3.1). We present the distribution of maximum time reached in Fig. 4.2a, and the total colony size as a function of maximum time reached in Fig. 4.2b. In some simulations, the queen died due to natural mortality; those simulations ranged in the maximum number of time steps reached and in the resulting colony size at collapse (Fig. 4.2a,b). In the majority of runs ($n = 805/1,000$), simulations were halted because the maximum number of time steps had been reached, not because the colony had collapsed (Fig. 4.2a). In those simulations, the predicted total colony size ($F + N + B$) ranged from 3,456 to 3,815 ants (Fig. 4.2b, Table 4.2), in accord with baseline model predictions from Chapter 3 (Fig. 3.3).

Model predictions in the presence of *in-nido* parasitism

In the presence of *in-nido* parasitism ($\beta > 0$), colony collapse occurred readily, due to both queen death and death of a sufficient number of individuals to fall below the minimum colony size needed for functioning (Fig. 4.3, Table 4.2). We plot the distribution of maximum time reached for a range of β values in Fig. 4.3a; in Fig. 4.3b, we plot the total colony size reached at those maximum times. In the presence of *in-nido* parasitism and under a range of β ranging from 0.0001 to 1 days⁻¹, our model predicts colony collapse in all simulations in less than 200 days (5,000/5,000 simulations, Fig. 4.3a,b). In the majority of cases, colony collapse was due to colony size being reduced below the minimum threshold (4,953/5,000 simulations, Fig. 4.3b, Table 4.2); however, in a few cases colony collapse was due to queen death.

Changing cadaver contact rate, ψ

To assess whether social segregation could reduce epidemic spread, we manipulated the rate of cadaver contact for foragers F and nest workers N (ψ_F , and ψ_N) while holding β constant at 0.001 days^{-1} . While this value of β did cause colony collapse in all simulations when $\psi_F, \psi_N = 1/10$, when cadaver contact rates were lowered to values ranging from $\psi_F, \psi_N = 1/25$ to $\psi_F, \psi_N = 1/1000$, some colonies were able to survive (9-365/1000 simulations, respectively, Table 4.2), albeit with lowered colony sizes from that predicted in the absence of *in-nido* parasitism (Table 4.2). Due to the spatial organization of brood (B) and the queen (Q) inside ant colonies [152, 449], these compartments are unlikely to come into direct contact with infectious cadavers and we therefore did not explore the impact of changing their cadaver contact rates ψ_B and ψ_Q , respectively.

Changing cadaver decay rate, ζ

To assess whether the rate at which cadavers decay impacts model predictions of colony collapse, we varied the cadaver decay rate ζ from 0.33 days^{-1} to 24 days^{-1} , corresponding to cadavers remaining infectious inside the nest for 3 days to 1 hour, respectively. When cadavers remained in the nest for 3 days ($\zeta = 0.33 \text{ days}^{-1}$), only 0.12% of simulations had colonies surviving, with a mean colony size of 35.42 ants (Table 4.2). In contrast, if the cadavers decayed in less than 1 day ($\zeta > 1 \text{ days}^{-1}$), then the percentage of colonies surviving ranged from 23.9% to 81.1%. The size ranges for colonies that did survive depended on the cadaver decay rate, with cadaver decay rates of $\zeta = 6, 24 \text{ days}^{-1}$ yielding mean colony sizes of 606.18 and 2,086.36 ants, respectively (Table 4.2).

4.5 Discussion

Ant colonies are host to a diversity of parasitic organisms [91, 406]. However, parasites that are capable of within-nest transmission are few, and empirical observations of ant colony collapse have rarely been observed. Here, we investigated the epidemic potential of such *in-nido* parasites by employing a stochastic modeling approach. In the absence of parasitism, we found that the stochastic implementation of our model recapitulates the baseline results found in Chapter 3 (Figure 4.2). In the presence

of *in-nido* parasitism and under biologically plausible parameter values, colony collapse readily occurred, suggesting that such parasites could impose a strong selective pressure on ant colonies (Figure 4.3a,b).

While our preliminary modeling results suggest that colony collapse is likely, ant colonies are known to employ a suite of anti-parasite defenses that could serve to mitigate collapse (reviewed in [91, 97, 99, 129]). Behavioral defenses, such as grooming and isolating sick nest mates, have been shown to be particularly effective [60, 133, 146]. We additionally investigated whether two behavioral defenses, behavioral avoidance and cadaver management, could impact our model predictions of epidemic outcomes. Both defenses, employed in isolation, can reduce the probability of colony collapse, though colony size in the presence of *in-nido* parasitism is reduced (Table 4.2).

Through avoiding contact with infectious material, ants can limit colony-wide exposure. The exact mechanisms underlying the potential behavioral avoidance of healthy ants and dead cadavers remain unclear; many ants may be able to avoid infectious cadavers due to spatial structuring within ant nests. Task specialization and the division of labor within colonies may also mean that only a small subset of individuals are relegated to roles that would put them in contact with potentially infectious cadavers [5, 151]. Thus, our current model, which makes coarse assumptions about the relative contact rates of foragers, nest workers, brood, and the queen with infectious cadavers, may overestimate the impact of *in-nido* parasitism. Future work will explicitly include a compartment for corpse-tenders, and the comparison of models with and without this additional compartment will allow us to explore how the division of labor within ant colonies could serve to mitigate disease transmission.

The preliminary results in this chapter also highlight that effective cadaver management likely plays a very important role in preventing disease outbreaks within ant and other social insect colonies. Chouvenc and Su (2012) found that no epizootics occurred in sub-colonies of the termite *Coptotermes formosanus*, because the termites were able to cannibalize and bury the cadavers of infected nest mates before they became infectious [454]. Recent work has shown that ants are able to chemically disinfect cadavers with formic acid, rendering spores unable to germinate (E. Solá Gracia, personal communication). Indeed, empirical work has shown that in instances where the ability to perform sanitary behaviors is compromised, epidemics within nests can occur [438].

Ant colonies have a suite of physiological and behavioral immune mechanisms in

their arsenal (reviewed in [91, 97, 99, 129]), and many of these mechanisms were likely present prior to their transition to group living [92]. Ants are host to some parasites that are capable of within-nest (*in-nido*) transmission, and this work theoretically demonstrates that such parasites are capable of causing colony collapse (Fig. 2.3). However, this work also suggests that the anti-parasite defenses ants have, particularly social segregation and cadaver management, may allow them to mitigate the potential for colony collapse, confirming findings from empirical studies.

Acknowledgements

We would like to acknowledge Emilia Solá Gracia for insightful discussions about ant cadaver management.

4.6 Figures and Tables

Figure 4.1: Schema for the model of colony growth in the presence of *in-nido* parasitism.

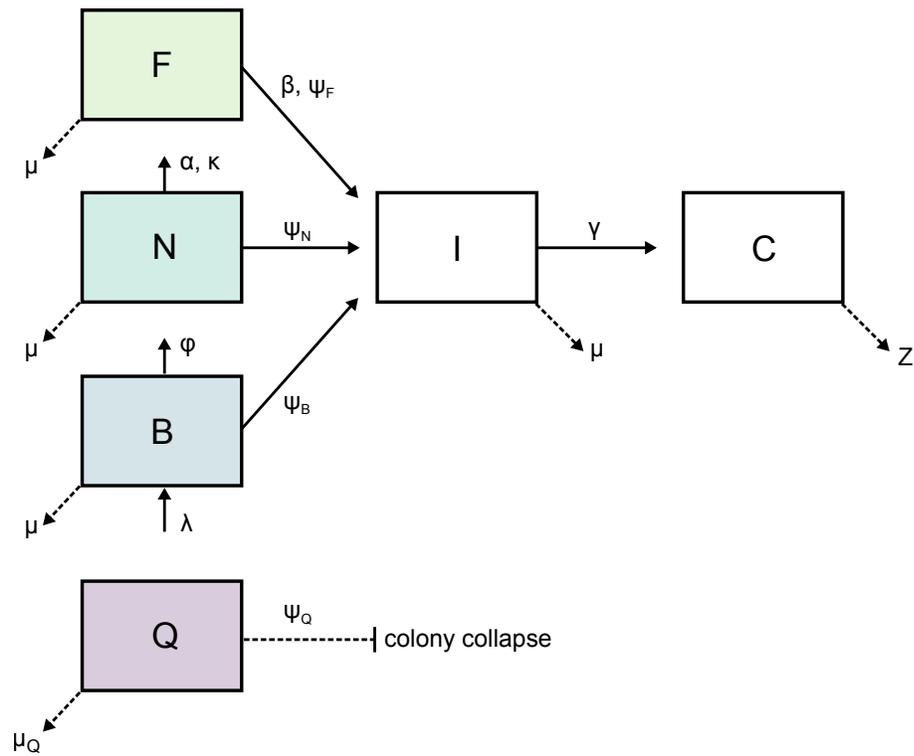


Figure 4.2: Model predictions under baseline conditions and in the absence of *in-nido* parasitism.

(a) Density plots of maximum time reached in a given simulation. In some simulations, the queen died stochastically due to her own natural mortality rate, resulting in colony collapse (green). In the majority of simulations, colonies did not collapse and the maximum time simply reflects the maximum number of time points allowed for simulation runs. (b) Total colony size as a function of maximum time reached in a given simulation. The majority of colonies did not collapse (purple) and their colony sizes ranged from 3,456 - 3,815 ants (Table 4.2).

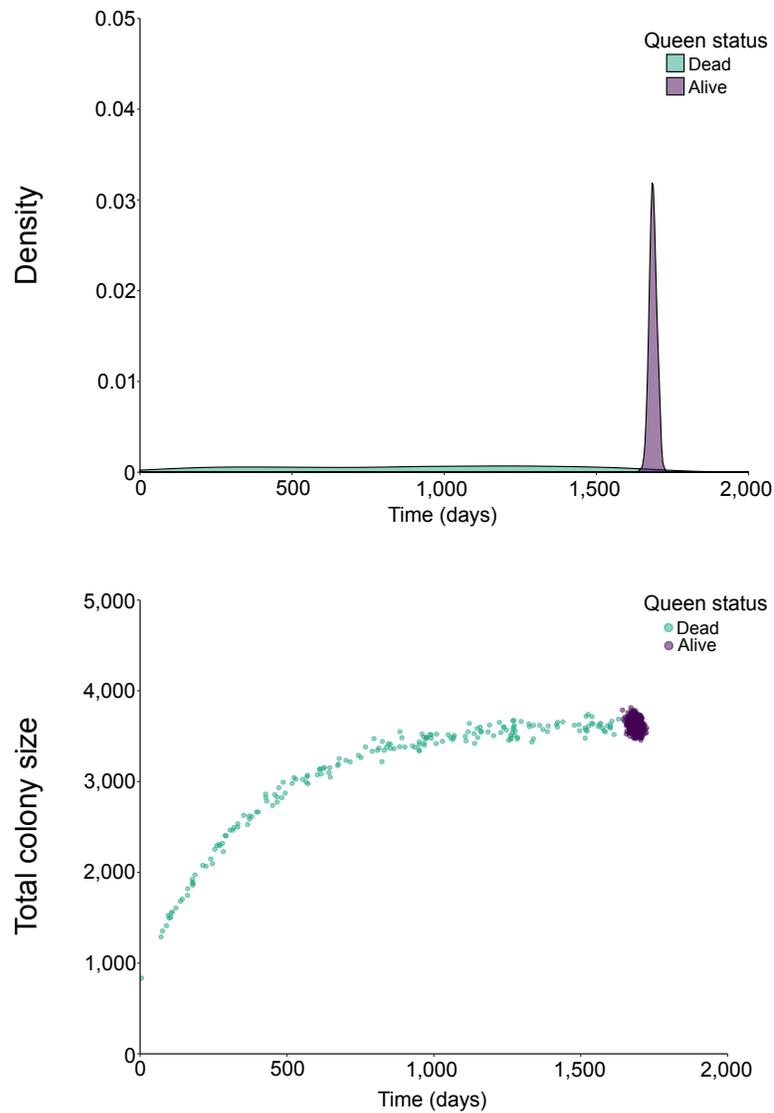


Figure 4.3: Model predictions under changing values of the parasite force of infection, β .

(a) Density plots of maximum time reached as a function of changing values of β . For values of $\beta > 0.01 \text{ days}^{-1}$, colony collapse occurred in all simulations in less than 25 days. (b) Total colony size ($F + N + B$) as a function of maximum time reached and β . All simulations resulted in collapse, mostly due to colony sizes dropping below the minimum threshold, σ .

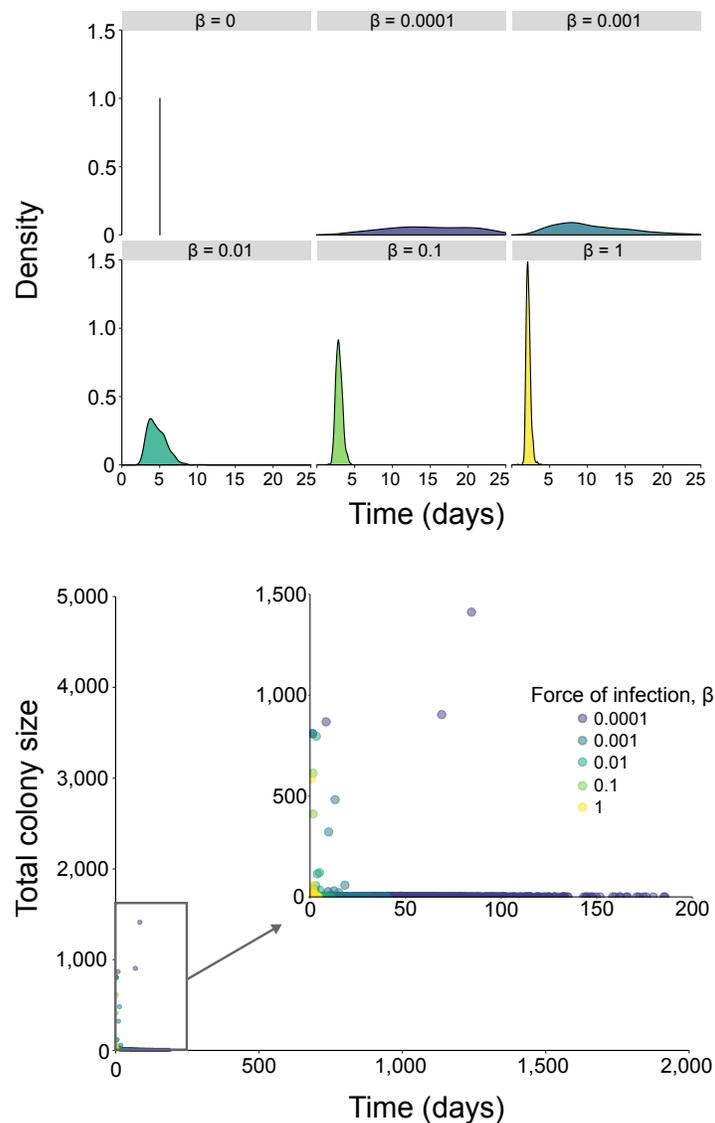


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Phi, ϕ	days ⁻¹	Brood - nest worker transition rate	-	1/56
Alpha, α	days ⁻¹	Nest worker - forager transition rate	-	0.1
Kappa, κ	-	Max proportion of the colony in the forager compartment	-	0.3
Sigma, σ	ants	Minimum colony size	-	10
Mu, μ	days ⁻¹	Natural mortality rate	-	1/365
Mu, μ_Q	days ⁻¹	Natural mortality rate of queen	-	1/(365*25)
Gamma, γ	days ⁻¹	Parasite-induced mortality rate	-	1/7
Beta, β	days ⁻¹	Per-capita parasite transmission rate	0.0001 - 1	0.001
Psi, $\psi_{F,N}$	days ⁻¹	Cadaver contact rate	0.001 - 0.1	-
Psi, $\psi_{Q,B}$	days ⁻¹	Cadaver contact rate	-	0.0001
Zeta, ζ	days ⁻¹	Cadaver decay rate	0.33 - 24	1

Table 4.2: Modeling results: colony collapse and colony sizes.

Model predictions for the number of simulations which did not collapse and their mean colony size as a function of varying values of β , $\psi_{E,N}$, and ζ . Model predictions are from numerical simulation under baseline parameter values given in Table 4.1 and are out of 1,000 simulations per parameter set.

Model predictions					
Parameter	Value	Colonies w/ Q alive	N. colonies surviving	Mean colony size	Colony size range
Baseline	-	805	805	3623.596	3456 - 3815
β (days ⁻¹)	0.0001	991	0	-	-
	0.001	985	0	-	-
	0.01	993	0	-	-
	0.1	993	0	-	-
	1	991	0	-	-
$\psi_{E,N}$ (days ⁻¹)	0.1	992	0	-	-
	0.04	936	9	25.33	18 - 33
	0.02	321	202	52.60	25 - 101
	0.01	276	276	103.23	54 - 177
	0.004	273	273	252.14	158 - 447
	0.002	329	329	509.36	316 - 902
	0.001	365	365	977.53	731 - 1304
ζ (days ⁻¹)	24	819	819	2086.36	1773 - 2351
	6	724	724	606.18	370 - 955
	3	621	621	306.19	179 - 711
	2	497	497	201.57	122 - 395
	1.33	353	353	133.52	76 - 224
	1	239	239	103.28	60 - 218
	0.67	146	140	68.46	43 - 103
	0.5	136	57	52.75	31 - 89
	0.4	231	26	43.19	26 - 75
	0.33	405	12	35.42	21 - 48

**Ant colony social, spatial, and temporal organization
in the absence of disease**

5.1 Abstract

High-density living is often associated with high disease risk due to density-dependent epidemic spread. Despite being paragons of high-density living, the social insects have largely decoupled the association with density-dependent epidemics. It is hypothesized that this is accomplished through prophylactic and inducible defenses termed ‘collective immunity’. Here we characterize segregation of carpenter ants that would be most likely to encounter infectious agents (i.e. foragers) using integrated social, spatial, and temporal analyses. Importantly, we do this in the absence of disease to establish baseline colony organization. behavioral and social network analyses show that active foragers engage in more trophallaxis interactions than their nest worker and queen counterparts and occupy greater area within the nest. When the temporal ordering of social interactions is taken into account, active foragers and inactive foragers are not observed to interact with the queen in ways that could lead to the meaningful transfer of disease. Furthermore, theoretical resource spread analyses show that such temporal segregation does not appear to impact the colony-wide flow of food. This study provides an understanding of a complex society’s organization in the absence of disease that will serve as a null model for future studies in which disease is explicitly introduced.

5.2 Introduction

Social insects are paragons of self-organized complex systems [58, 458–461]. Individuals interact to produce sophisticated colony-level behavior that is more than, and not necessarily predictable from, the behavior of the individuals that create it [58]. This emergent behavior, such as honeybees ‘democratically’ choosing between nest sites [462] or ants creating elaborate living architectures in response to environmental obstacles [463], has likely contributed to the ecological success of the social insects as a whole. Therefore, it remains imperative to understand how behaviors at the scale of the individual and at the scale of the colony dynamically influence each other, especially given the importance of functional roles in social insect colonies [464]. Such understanding is salient in the face of perturbation, where changes at the individual level due to disease or predation may have cascading consequences for the entire colony.

Disease is an especially relevant perturbation for social insects because it has been suggested that a significant cost of high-density living is increased disease risk [1–3, 73, 91, 465]. Though social insect colonies have both higher density and a higher average genetic relatedness than other animal groups [38], their ecological dominance over significant evolutionary time [38] suggests that they appear to have effectively adapted to mitigate the presumed negative cost of disease. This is not because they lack infectious agents- social insects are host to a wide array of pathogens and parasites ([2, 22, 91, 127], Appendix A.1), that have several means of gaining entrance to and spreading within the colony. Rather, social insects are thought to mitigate intense infection pressures through a series of standing and inducible defenses termed ‘social’ or ‘collective’ immunity [97, 128, 129]. These defenses range from the immunological to the behavioral, including how colonies are spatially organized and which tasks are allocated to different workers [129, 154, 466, 467].

The social and spatial segregation of workers most susceptible to encountering infectious agents is often cited as a mechanism of disease prophylaxis in social insect colonies [129, 156, 468]. However, many of these workers (i.e. foragers) are also responsible for the delivery of beneficial substances, such as food and antimicrobial compounds (e.g. tree resin) [469] into the colony and such segregation could impact the flow of beneficial resources [470]. Indeed, even seemingly harmful interactions, such as engaging in trophallaxis or allogrooming with a nest mate that has been ex-

posed, can lead to the transfer of either potential immune elicitors [132] (passive immunity) or low doses of inoculate that can lead to the mounting of a protective immune response [133] (active immunity). This is complicated further by the fact that the cost-benefit ratio of interacting with an exposed nest mate likely depends on the host-pathogen system involved [140]. Thus, understanding how colonies have balanced the opposing demands of maximizing the spread of beneficial resources while minimizing the transmission of pathogens leading to disease remains an important aim in studies of both social insects and social organisms as a whole.

A first step to understanding this balance in social insects is to determine if the social and spatial segregation of foragers does indeed occur in the absence of disease. Empirical work done in the past two decades have investigated various aspects of social insect colony organization through social and spatial lenses (Table D.1). Many studies have used proximity networks [471–473] to understand worker spatial segregation. Exciting technological advances have revolutionized the resolution with which we can measure social insect spatial segregation [152, 153] and these studies have also confirmed the relative segregation of workers performing tasks outside the colony from those remaining within. Network studies based on social interactions rather than just spatial proximity have been harder to come by, as observing individual behavior within a realistic colony setting remains a formidable task. Of those studies that have explicitly measured social interactions, antennation networks have been used to investigate how colony organization impacts information flow [464, 474] and trophallaxis networks have also revealed evidence for ‘organizational immunity’ in colony food flow patterns [475–477]. Most recently, analytical advances have allowed for the inclusion of temporal information in such social networks [470, 474]. Understanding the timing of interactions is crucial for accurately understanding how food, information, and disease dynamically flow through social insect colonies.

Thus, while we have been acquiring knowledge of colony organization across many different social insect systems, we haven’t yet integrated this work across social, spatial, and temporal scales in a single study system. What would be useful now is a system in which such integration exists that can be manipulated through experimental infection in subsequent work. To that end, here we characterize the basis for standing organizational immunity through forager segregation in colonies of the black carpenter ant, *Camponotus pennsylvanicus*, using a suite of social, spatial, and temporal analyses. The ant *C. pennsylvanicus* is widespread in the northeastern USA and has evolved

to nest inside dead trees [478]. We mimic this by maintaining colonies inside wood under complete darkness.

We first classify ants into functional categories based on whether they are performing or have previously performed tasks outside the nest (which translates to elevated disease risk). Next, we look at the oral exchange of food (trophallaxis) as the key social interaction of interest because colonies must balance efficient resource flow (food, antimicrobial compounds, information) with mitigating disease spread [474]. If social segregation does occur, we would expect to see its signature represented in the trophallaxis interactions between ants that have been outside and those that have remained buffered within the relatively protected confines of the colony [97]. To facilitate comparison of how trophallaxis between ant functional groups could impact potential disease risk, we borrow the concept of ‘person-time’ used in calculating epidemiological incidence rates [479]. Next, we incorporate individual movement data to assess whether spatial segregation is present in the absence of disease. Finally, we incorporate the time-sensitive ordering of social interactions to understand how observed colony organization serves simulated resource flow through *C. pennsylvanicus* colonies. Integrating this suite of approaches shows that ant colonies are indeed segregated, though in a way more nuanced than previously theorized. Our work serves as a useful null model of a complex social insect society in the absence of perturbation.

5.3 Methods

5.3.1 Ant colony set-up and filming

Two queen-right *C. pennsylvanicus* colonies were collected from field sites in Centre County, central Pennsylvania, U.S.A. in December 2012. Seventy-five worker ants were selected from each colony and were individually labeled. Labels consisted of numbers printed on photo paper that were affixed to the ants’ posterior abdomens (gasters) with optically clear nail polish. Following a 5-minute acclimatization period, the labeling was not observed to alter the ants’ behaviors, movement or interactions.

The labeled ants and the queen were housed in a nest set-up consisting of a four-chambered wooden nest (total area = 63 cm²) that was gridded to a resolution of 1cm² and covered with a plexiglas top. The nest was contained within a filming box so that nest conditions were always dark. The nest was separated from a sand-bottomed

foraging arena (total area = 144 cm²) by a 4-m long maze. The length of the maze was observed to create a clear separation between workers allocated to foraging versus internal colony tasks. Inside the foraging arena, ants had ad libitum access to water, 20% sucrose solution and a protein source (mealworms).

Each colony was filmed for approximately 30 minutes beginning at 21:00 hrs for 8 consecutive nights in June 2013 using a GoPro Hero2 camera with a modified IR filter (RageCams.com) illuminated under infrared light. Ants cannot detect infrared light, so the set-up was similar to the dark within-nest conditions that they naturally experience.

Video analysis and trophallaxis measurements

For each night of filming, all trophallaxis interactions of each individual ant inside the nest were recorded for a 20-minute observation window. A trophallaxis event was recorded when ants engaged in mandible-to-mandible contact for greater than 1s. A liquid food bubble transferring between the two individuals was usually observed accompanying this behavior. While knowing the directionality of food exchange is important, it could not always be established through our observations and thus we do not analyze directionality. All together, the filming led to 401 hours of observation (76 ants x 2 colonies x 0.33 hours x 8 nights). The identities of the individuals interacting, the start and stop time of their trophallaxis interaction, and the grid location of their interaction within the nest was recorded. Additionally, the overall functional classification of every ant during each observation period was recorded (i.e. active forager, inactive forager, nest worker, queen- see below).

5.3.2 Ant functional categorization

Nest workers were ants that were never observed to leave the nest in the current or any previous observational periods. Active foragers were ants that actively entered or left the nest during the observation. Inactive foragers were ants that had been observed leaving the nest on previous nights, but which did not leave the nest during the current 20-minute period in which they were being analyzed. Here 'inactive' simply refers to the fact that those ants were not actively outside the nest during the current observation period. It does not imply overall behavioral inactivity. The functional categorization of an individual each night changed based on what they

were doing in that observation period as well as what their behavioral history over previous observations had been (i.e. once an ant has been observed foraging, it can no longer be classified as a ‘nest worker’).

5.3.3 Trophallaxis count and duration

The number of trophallaxis events and their duration for each individual was recorded as above. To test for differences in mean trophallaxis count and duration as a function of ant functional classification (i.e. active forager, inactive forager, nest worker, or queen), two-sided Kruskal-Wallis one-way analysis of variance tests (hereafter, ‘K-W’) were conducted using the `kruskal.test` function in R [457] (Fig. 5.1, Table D.2a). For K-W tests that were statistically significant ($p < 0.05$), Dunn’s tests coupled with a Benjamini-Hochberg correction for multiple hypothesis testing were then used to determine which functional classes had significant pair-wise differences (Table D.2b). Data from all nights of observation were pooled together, but each colony was analyzed separately.

5.3.4 Static network analysis and visualization

Unweighted, undirected static network analyses were conducted using the `iGraph` package implemented in R [457,480], such that only the number of discrete trophallaxis events and not their duration was used in the analysis. Network analyses were aimed at identifying whether key individuals that could serve as brokers or attenuators of food and/or disease flow were associated with a particular ant functional class; metrics analyzed included degree, betweenness centrality, closeness centrality, and Burt’s constraint [481, 482]. Degree is the number of connections that an individual ant has to other ants. Betweenness centrality is an estimate how important an individual ant is to promoting connectivity across the entire colony [482] and is measured by the number of times an individual acts as a bridge along the shortest path between two other ants. Closeness centrality is based on the distance (measured by shortest paths) from an individual to every other individual in the colony [481]: the more central an ant is, the lower its total distance is from all other ants. Burt’s constraint is a more nuanced measure to qualify; it measures the extent to which an ant’s interaction partners are redundant and thus identifies which ants could act as brokers of food or disease between ‘structural holes’ in a network [483].

These metrics were analyzed separately for each individual in each colony for each night of observation. Kruskal-Wallis tests were used to test whether there were differences in these metrics between ant functional groups because these metrics were not normally distributed (Table D.3b). On metrics in which the K-W tests were statistically significant ($p < 0.05$), Dunn's tests with p-values adjusted using a Benjamini-Hochberg correction were performed to assess which functional groups were significantly different from one another (Table D.4).

Trophallaxis networks were visualized using the circular layout in GEPHI [484], in which circles represent individual ants (Fig. D.1). Each ant was assigned a position based on its tracking ID that was maintained in all visualizations for all nights; trophallaxis interactions between ants are represented as lines (edges) between the respective circles. The length of an edge conveys no information, but the width of a given edge is proportional to the number of distinct trophallaxis interactions those ants had during that night of video observation.

5.3.5 Functional group networks

To better understand the functional connectivity of the ant trophallaxis networks, we constructed functional networks by collapsing each ant functional group (active foragers, inactive foragers, nest workers, queen) into nodes and representing the total duration of all interactions between each group as connections between nodes (weighted edges) (Fig. 5.2a,b). Here, the width of edges is proportional to the total duration of trophallaxis spent between those two functional groups and these are thus weighted network graphs.

Ant-time calculation

While the total duration of trophallaxis (edge weight) in the ant functional group networks are the same for each group in the interacting pair, this time actually represents variable per-capita disease transmission risk due to different numbers of ants in each functional group and variable amounts of time in the nest for the active forager class. Thus, to get a more accurate understanding of how trophallaxis duration corresponds to potential per-capita transmission risk, we standardized these total trophallaxis durations using the epidemiological concept of 'person-time' [479], hereafter referred to as 'ant-time'. For a detailed explanation of how ant-time was calculated, please refer

to C.1.

Proportion of time-budget engaged in trophallaxis

Having calculated the ant-time for each class for each night, the percentage of each functional group's total time-budget engaged in trophallaxis was calculated. The total duration of trophallaxis (edge weight) between two ant types provides the numerator and this is the same for both functional groups in the dyadic interaction being considered. However, the ant-time denominator varies for each type and thus the same total trophallaxis duration represents different total percentages of each group's total time-budget available for interaction. The percentage time-budget for each dyadic interaction (for example, active forager - active forager, active forager - inactive forager, active forager - nest worker, active forager - queen) is presented in Fig. 5.3. For percentage of time-budget engaged in trophallaxis, refer to Table D.5.

Ant functional network sub-graphs

Understanding the functional connectivity between active foragers, inactive foragers, nest workers and the queen is important for a broader understanding of how resource and disease flow is accomplished in carpenter ant societies. To facilitate comparison of these functional networks across nights and between colonies, we categorized the empirically observed network sub-graphs. Network sub-graphs are the different patterns of connection that can occur between nodes and provide an overview of global network structure [485]. The full range of possible network sub-graphs for a 4-node network (i.e. active forager, inactive forager, nest worker, and queen) with varying numbers of connections (i.e. 1-6 edges) and the network sub-graphs that were empirically observed are given in Fig. 5.2c.

To compare the observed network sub-graphs to those expected under a null model (i.e. trophallaxis connections within the colony are formed randomly), we generated simulated networks. Since there were both differing numbers of individuals in each functional category and differing numbers of interactions for each night, all network sub-graphs are not expected to be equally realized. We generated randomized networks that preserve the same number of edges, degree distribution, and number of individuals in each ant functional class by rewiring the edges of each empirical network using double-edged swaps [486] (implemented by iGraph's 'rewire' function;

self-loops were not permitted). For each night, we performed 500 random edge swaps to produce a new, randomized network realization. We did this 100 times per observed night to generate a histogram of expected ($N=1,600$) versus realized ($N=16$) sub-graphs, given in Fig. 5.2d.

5.3.6 Spatial movement analysis

Five known forager ants (here, active foragers and inactive foragers are grouped because individuals often transitioned between those categories over the eight nights of observation), five randomly selected nest workers, and the queen were chosen from each colony for additional spatial movement analysis. The wooden nest in which ants were housed was gridded to a resolution of 1cm^2 , and the cell locations where the majority of the ant's body was located as well as the time stamp when it was in that location were recorded for each observation period. The residence time spent in each cell was recorded to determine nest spatial use; this aggregated residence time is given in Fig. 5.4. This data was used to fit a continuous-time discrete space random walk model (see model description, Appendix C.1) for ant movement behavior [487, 488], with the goal of identifying the relative spatial movement of foragers (active and inactive) vs. nest workers and the movement behavior of these groups (location and speed) around the queen.

5.3.7 Simulated resource spread

Interactions from the static networks were analyzed with the additional inclusion of interaction time-stamps. Temporal networks were constructed using the package 'timeordered' [489] implemented in R (Fig. D.2). To understand how the pattern and timing of social interactions converge to impact the flow of food or disease, a resource-spread analysis was conducted using the spreadanalysis function in the 'timeordered' package. Using the empirical temporal networks, the spreadanalysis function randomly chooses an individual and 'seeds' it with a hypothetical resource at time 0. Then, using the time-ordered network interactions that were actually observed, the function simulates the fraction of the entire network reached by the theoretical food source through first-order, second-order, third-order etc. interactions at various time intervals. Here, we specified 100s time intervals and the use of 20 randomly chosen individuals for each colony-night combination. The mean fraction of the

network reached at each interval as a function of ant functional classification was computed for each colony averaged over all nights of observation and is given in Fig. 5.5.

5.4 Results

5.4.1 Individual trophallaxis count and duration

There was a significant difference in the number of distinct trophallaxis events between ant functional groups in one colony (colony 1: $\chi^2 = 20.34$, $p < 0.0002$, two-sided K-W test, Fig. 5.1, Table D.2a). Active foragers engaged in more trophallaxis events than the queen (z-statistic = -2.92, $p < 0.004$, Dunn test, Table D.2b). In colony 1, inactive foragers engaged in more trophallaxis events than did either nest workers or the queen, (z-statistic = -3.420, -3.324 and $p < 0.002$, $p < 0.002$ nest workers and queen, respectively, Dunn test, Fig. 5.1, Table D.2a) but there was no significant difference between active foragers and inactive foragers [z-statistic = -0.197, $p = 0.4216$, Dunn test, Table D.2b]. In colony 2, trophallaxis count was not significantly different between ant functional groups ($\chi^2 = 7.282$, $p = 0.063$, two-sided Kruskal-Wallis test, Fig. 5.1, Table D.2a). The duration of these trophallaxis events was not statistically different between ant functional groups in either colony (colony 1: $\chi^2 = 6.4096$, $p = 0.0933$, colony 2: $\chi^2 = 4.386$, $p = 0.2227$, two-sided K-W test, Table D.2a.)

5.4.2 Static network analysis

Static, undirected networks for each colony for each night of observation are presented in Fig. D.1. We tested for differences in network metrics aggregated over all nights between the different groups (active foragers, inactive foragers, nest workers, and queen). Active foragers and inactive foragers had a higher mean degree centrality (number of unique individuals interacted with, Table D.3a) compared to nest workers in both colonies (Active foragers colony 1: z-statistic=-2.514, $p < 0.02$, colony 2: z-statistic=-2.4918, $p < 0.02$; inactive foragers colony 1: z-statistic=-4.432, $p < 0.0001$, colony 2: z-statistic=-3.836, $p < 0.0005$, Dunn test, Table D.4), but they are not significantly different from each other (colony 1: z-statistic = -0.4747, $p = 0.3175$, colony 2: z-statistic = -1.4411, $p = 0.1122$, Table D.4). While the queen had a median degree of 1,

the identity of the individual she interacted with was not consistent across all nights in either colony. In colony 1, the closeness centrality of inactive foragers was significantly lower than that of nest workers (z-statistic=3.391, $p < 0.00001$, Dunn test, Table D.4), which indicates that in that colony inactive foragers are more socially central on average than other colony members. There were no significant differences in closeness centrality between ant types in colony 2 ($\chi^2=3.868$, $p=0.2761$, K-W test, Table D.3b). The Burt's constraint (redundancy of contacts) of the queen was significantly higher than that of active foragers and inactive foragers in colony 1 (z-statistic = 2.2875, 2.703, $p=0.0222$, 0.0206, respectively, Dunn test, Table D.4), but not significantly different in colony 2 ($\chi^2=3.7467$, $p=0.2901$, K-W test, Table D.3b).

5.4.3 Ant functional group networks

Of the 59 possible ant functional group network motifs, only 4 motifs were empirically observed in the 16 nights of observation across both colonies (Fig. 5.2c). Of these, 2 motifs in particular (motifs 2B, 3N) accounted for 87% of all empirically observed motifs. While the observed network motifs fall within those predicted to occur assuming random interactions between ant functional categories (Fig. 5.2d), whether these occur statistically more often than would be predicted cannot be tested as there is no variance available for the realization of each night's empirical network.

5.4.4 Percent time-budget calculations

The percent time-budget each functional class engaged in trophallaxis with all other ant functional classes is given in Table D.5. Taking the ant-time of each functional class into account provides a more nuanced view of ant group interactions for the individuals within those functional groups. While interactions with the queen represent a small fraction of the total trophallaxis happening inside the nest (1.66% +/- 2.85% and 1.46% +/- 2.2%, colony 1 and 2 respectively), this was found to represent approximately 4-5% of her entire time budget across both colonies (5.5% and 4.17%, colony 1 and 2 respectively, D.5). This represents a greater percentage of time at risk than would be expected if just the duration of her trophallaxis events out of the whole colony were considered. In colony 2, active foragers spent an average of 25% of their time within the nest engaging in trophallaxis, compared to 5.82% for nest workers.

5.4.5 Ant movement and spatial analysis

The average spatial usage of foragers (active and inactive), nest workers, and the queen is given in Fig. 5.4. Foragers (active and inactive) occupied a greater proportion of the total nest space than did either nest workers or the queen. The queen was largely immobile in both colonies, though in one colony (colony 1), the queen spent some time in three of the four chambers of the nest.

Results of our movement analysis show that in colony 2 nest workers are more mobile (have higher movement rates) than foraging ants while the latter are in the nest ($p < 0.01$, two-sided T-test, Table D.6). This result does not hold in colony 1, and the overall effect size is small. There was no evidence of directional queen avoidance by foragers (active and inactive) or nest workers in either colony, but there was evidence in both colonies that foragers (active and inactive) move faster than nest workers when near the queen compared to when they are in another chamber ($p < 0.01$, two-sided T-test, Table D.6).

5.4.6 Simulated resource spread

Social network data has traditionally been analyzed as a time-aggregated or static graph (Fig. D.1) in which the timing and order of interactions is ignored. However, such timing and order is crucially important for dynamic flow processes, such as disease transfer [474]. Based on the timing of interactions, returning active foragers were never actually observed to interact in a way necessary for disease transmission to the queen (Fig. D.2, i.e. after an active forager has returned from a trip outside the nest). Spread analysis indicates that such temporal segregation does not appear to inhibit the simulated flow of food, with no apparent differences between the mean network fractions reached when seeded by different ant types in either colony. Food generated from active foragers and inactive foragers in colony 1 was able to reach a higher mean fraction of the network than food generated from either nest workers or the queen (Fig. 5.5). In colony 2, food seeded from an active forager initially reached a higher mean fraction of the network, but this converged to 25% by the end of the twenty minute observation period regardless of what functional class the food was seeded from.

5.5 Discussion

Interacting with foragers, both socially and spatially, is a necessary risk for ant colonies. Theory predicts that interactions between potentially exposed foragers (actively returning foragers and inactive foragers that have foraged in the recent past) and other classes (i.e. nest workers) should be minimized [97], but an integrated understanding of colony organization has remained elusive due to the inherent difficulties of observing within-colony social dynamics. Our behavioral analyses show that active foragers engage in more trophallaxis interactions than nest workers (approximately 2 additional interactions, Fig. 5.1a,b). Static social network analyses complement these findings; in addition to engaging in more trophallaxis events (higher degree), foragers (active and inactive) exchange food with a greater number of unique individuals (Table D.3), indicating that their contact redundancy is lower than theory would predict [97, 468].

Re-analyzing the static network data through ant functional group networks (Fig. 5.2a,b), in which trophallaxis connections are represented between functional groups rather than individuals, allows broader patterns of colony social organization to emerge. Importantly, it also facilitates network comparison across nights and colonies and likely reflects a scale of analysis more biologically relevant to whole colony functioning [464]. Two network sub-graphs predominate, accounting for 87% of those observed: inactive-nest-queen and forager-inactive-nest closed triad (Fig. 5.2c,d); these represent only two out of 59 possible patterns of functional group connection. From these sub-graphs, it appears that inactive foragers may play an important role as brokers of trophallaxis in carpenter ant colonies, and that active foragers are interacting with nest workers more than might be expected.

This becomes even clearer when ant-time standardization is taken into account. When the higher abundance of nest workers is taken into account, active and inactive foragers spend a greater per-capita percentage of their total in-nest time budget actually engaged in trophallaxis (Table D.5). While this is an intuitive finding should they only be spreading beneficial resources, this is less intuitive given the variety of material that can be spread through intimate social contact in social insect colonies. Thus, this finding sheds light on the balance of constraints that have shaped the structure of carpenter ant social structure over evolutionary time. This suggests that under conditions in which perturbation is not present through disease or resource

competition, organizational immunity is not accomplished through simply reducing trophallaxis with potentially exposed members. Future studies in which the balance is empirically ‘tipped’ in favor of disease transmission will shed light on how malleable this social structure is in the face of acute perturbation.

In addition to the social position of foragers within the colony, we were also interested in how they spatially occupied their nest environment. Analysis of nest spatial usage showed that foragers (active and inactive) use more nest area relative to both nest workers and the queen (Fig. 5.4). While the queen’s lack of movement synchronizes well with predictions from social immunity (i.e. to be secluded) the expansive movement of the foragers is counter-intuitive. It is reasonable to assume that foragers should avoid internal areas of the nest [97, 129] but we did not observe this (Fig. 5.4). However, we found evidence in both colonies that foragers could be modulating their speed in response to their social environment (Table D.6). When foraging ants were in the same chamber as the queen, they moved faster than their nest worker counterparts. Such speed modulation could potentially reduce the impact of pathogen transmission to which foragers may have been exposed by moving faster near the most important individuals (i.e. queen, younger workers). This has not been previously considered as a mechanism to mitigate disease spread within the nest. Future studies that specifically address whether different ant classes alter their speed in response to different social environments inside the nest and what, if any, biological impact this has for potential disease transmission are needed.

The static network analyses of colony social organization and the spatial movement of foragers reveal that active and inactive foragers engage in more trophallaxis interactions and occupy a great spatial area within the nest than their nest worker and queen counterparts. This would appear counter to the verbal models of social immunity where intuition, without within-nest behavioral data, has suggested a stronger segregation between worker types, especially foragers [97]. In considering social immunity, however, time has been a previously neglected component [129]. In our data, when the timing and order of trophallaxis interactions are taken into account, active and inactive foragers and the queen never interact in a way that could lead to the biologically meaningful transfer of disease (i.e. after a forager has come back into the nest after a foraging trip, carrying some pathogen that might transfer to the queen via either oral food exchange or prolonged physical contact). Thus, the timing of social interactions provides additional evidence for nuanced organization within *C.*

pennsylvanicus colonies.

Infectious agents are not the only pressure that ant colonies face. Since trophallaxis interactions are a conduit for disease and food (and other material, see Introduction), there is a fundamental trade-off in optimizing food flow while minimizing disease spread, both of which are brought into the colony by foragers [91]. This trade-off is of interest because it could impact colony functioning even in the absence of disease; the temporal segregation of foragers could prolong the time it takes for incoming food to reach other colony members. Simulations of resource spread over the empirically observed trophallaxis networks (Fig. 5.5) provide an understanding of the flow trade-off that could result from temporal segregation of foraging ants. In both colonies the mean fraction of the network reached a high of 20-25% after 20 minutes. In colony 1, this was achieved in food originating from active and inactive foragers, showing that their temporal segregation did not appear to impact the potential flow of food. In colony 2, food saturated at this percentage regardless of what ant type it originated from.

Our study also highlights the need to consider an ant's behavioral past when considering its present and future role in colony functioning and the introduction of disease risk. Active foragers who have just returned from outside the nest are clearly capable of introducing potential pathogens into the colony. What remains unclear is for how long they remain capable of transmitting disease- at what point does a potentially infected incoming forager transition to an inactive forager no longer posing a threat? While the classification of inactive forager used here was defined by the methods of the study, there are clear behavioral differences between these ants and nest workers who have never been observed to leave the nest. Had they been included within the nest worker categorization, this would have obscured the network and spatial signals observed. We advocate that future studies of disease transmission in social insect societies follow individuals over a time period that will capture past exposure, and thus the continuum of foraging behavior and pathogen risk.

5.6 Conclusions

Through the incorporation of dyadic- and network-level social interactions, individual movement data, and the timing of social interactions, we have gained insights into how colony organization is accomplished in *C. pennsylvanicus* colonies. The standing

organization in an ant society, exemplified by the carpenter ant colonies studied here, appears to be more nuanced than previously imagined. Measuring social and spatial segregation in tandem is important because pathogens may have alternate means of gaining entry to, and transmitting within, social insect societies and it remains unclear to what extent spatial distance is a proximate mechanism underlying social distance. The timing of social interactions may provide an additional layer of disease prophylaxis in social insect societies. This adds evidence for the growing argument that temporal information and meaningful behavioral interactions should be included into social network analyses if we are to make biologically accurate conclusions [470, 490]. The temporal component of social interactions is especially worth future investigation because it is unclear to what extent pathogen infectivity and/or infective dose is reduced over time or multiple trophallaxis passages. Thus, social insect societies which employ living food ‘silos’ [477] may indeed be making use of such temporal protection.

Analyzing carpenter ant colony organization and functioning in the absence of disease and environmental heterogeneity provides a useful null model; we are now primed to study how these complex systems react to perturbation. Future experiments in which laboratory infections are combined with integrated social, spatial, and temporal approaches will further inform how social insect colony organization and individual behavior dynamically interact to reduce disease transmission. Social insects are host to a range of both generalist and specialist parasites [91], some of which can change the behavior of the infected host (i.e. *Ophiocordyceps*) or potentially alter the interactions between healthy and infected nest mates (i.e. *Beauveria*, *Metarhizium*), and some of which cause no discernible change in behavior. Such studies will also afford us the ability to synchronize theoretical predictions about disease transmission in societies from agent-based and SIR modeling approaches [155, 491] with empirical data from experiments in which disease can actually be introduced.

Acknowledgments

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Notes

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5.7 Figures and Tables

Figure 5.1: Trophallaxis count and duration.

(a,b) Trophallaxis count and (c,d) duration as a function of ant behavioral classification. Starred lines represent statistically significant differences between groups (Table S3b). Black lines represent the median values, boxes represent the range of values in the 1st through 3rd quartiles, and whiskers represent 1.5 times the inter-quartile range.

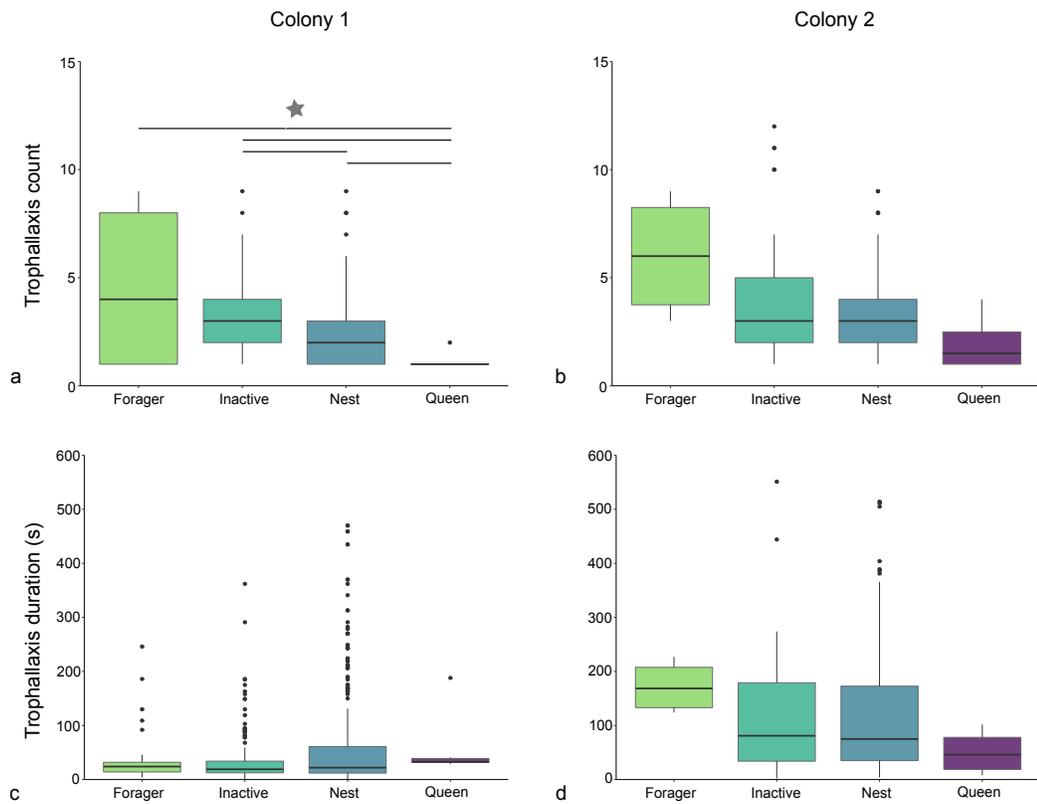


Figure 5.2: Ant functional networks.

(a) Representative ant functional group network showing trophallaxis interactions within and between ant functional groups. The total duration of all interactions between groups is given on the edge along with the percentage of the ant group's total time budget that this duration represents. (b) All ant functional group networks for both colonies over all nights. (c) All possible functional group interaction patterns (network subgraphs); blue shading indicates which subgraphs were actually observed over the eight nights of observation for both colonies. (d) Histogram of expected count of subgraph types under network randomization (grey) and the actual subgraph types realized in the study (blue).

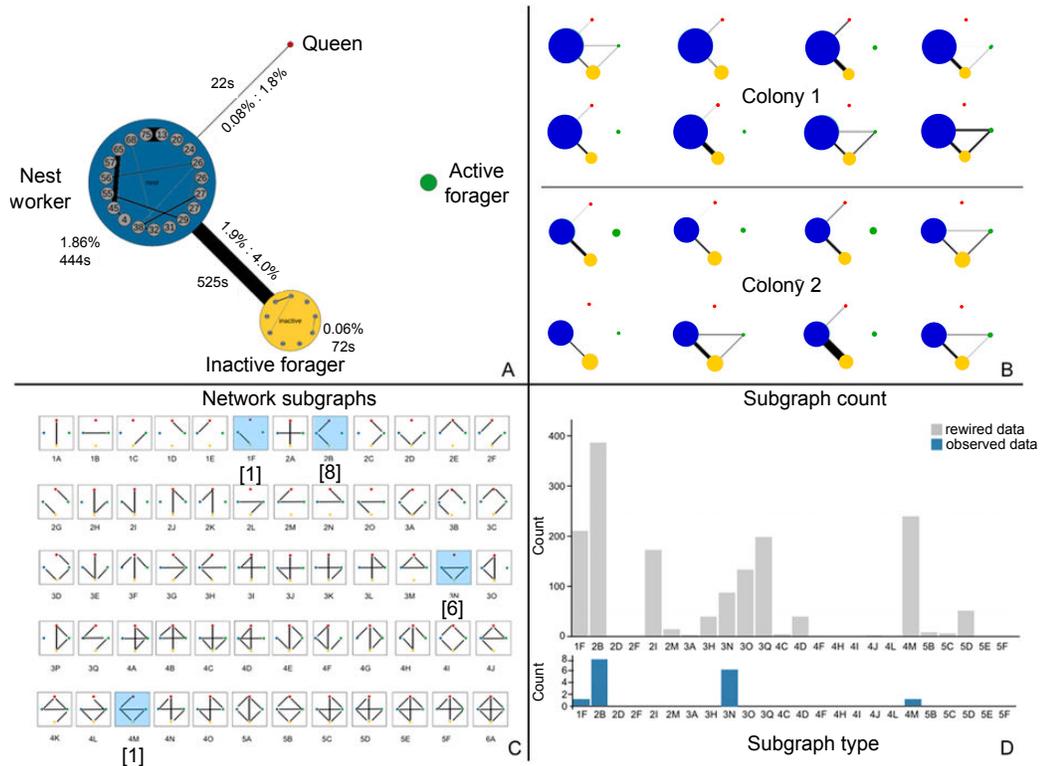
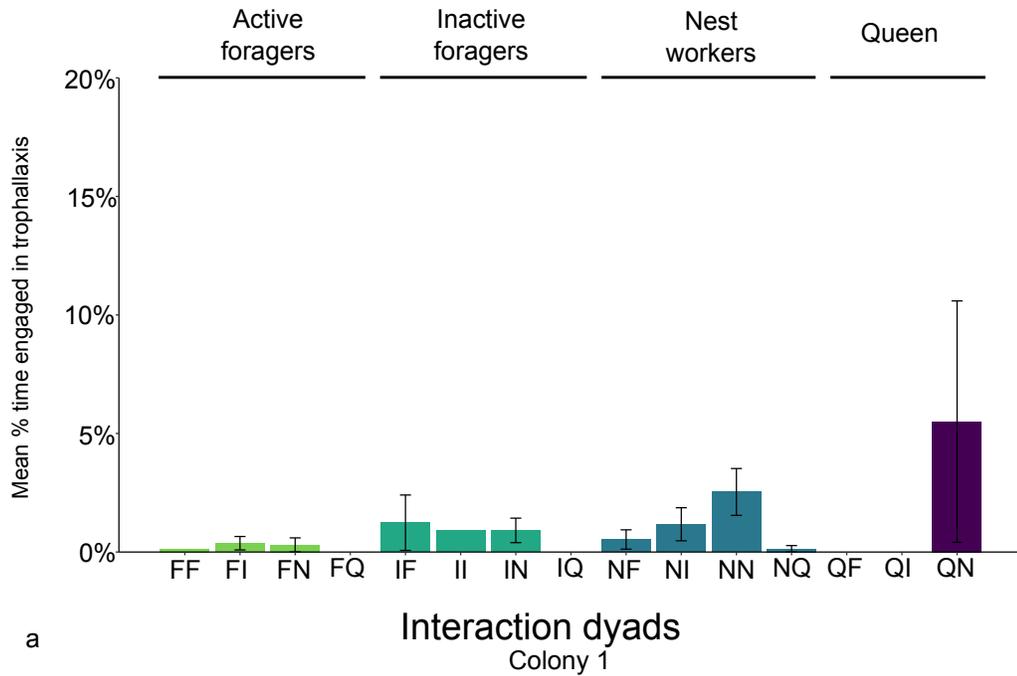
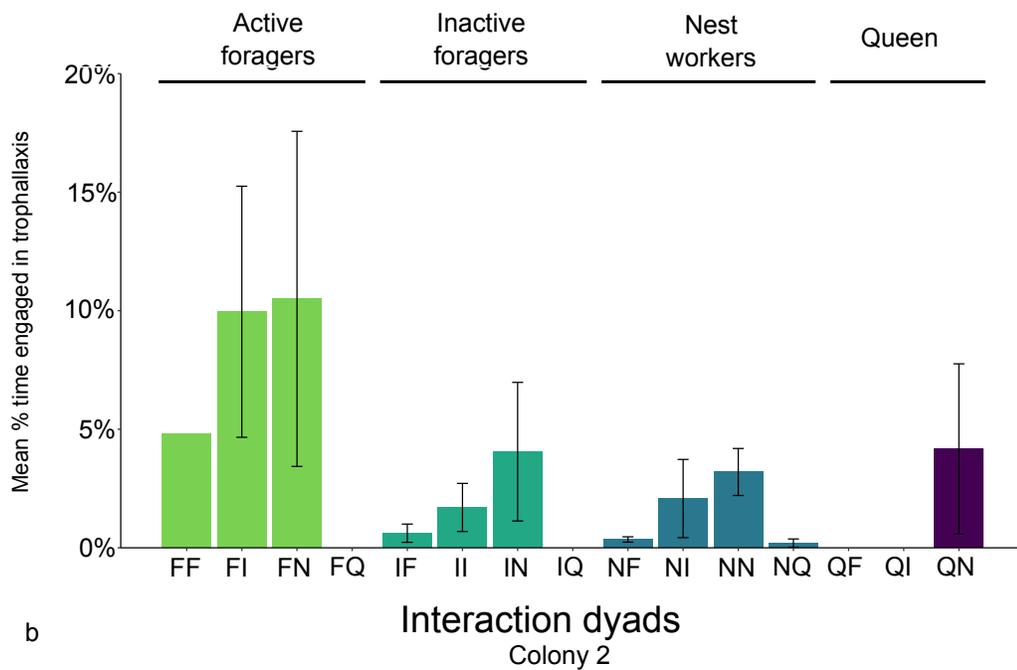


Figure 5.3: Trophallaxis as percentage of total ant-time budget.

Barplots showing the mean percentage of total time budget for each dyadic interaction between ant functional groups over all eight nights for each colony, error bars are \pm std. deviation.



a



b

Figure 5.4: Segregated use of nest space.

Aggregated residence times in ant-days for queens, foragers (active and inactive), and nest workers for colonies 1 and 2.

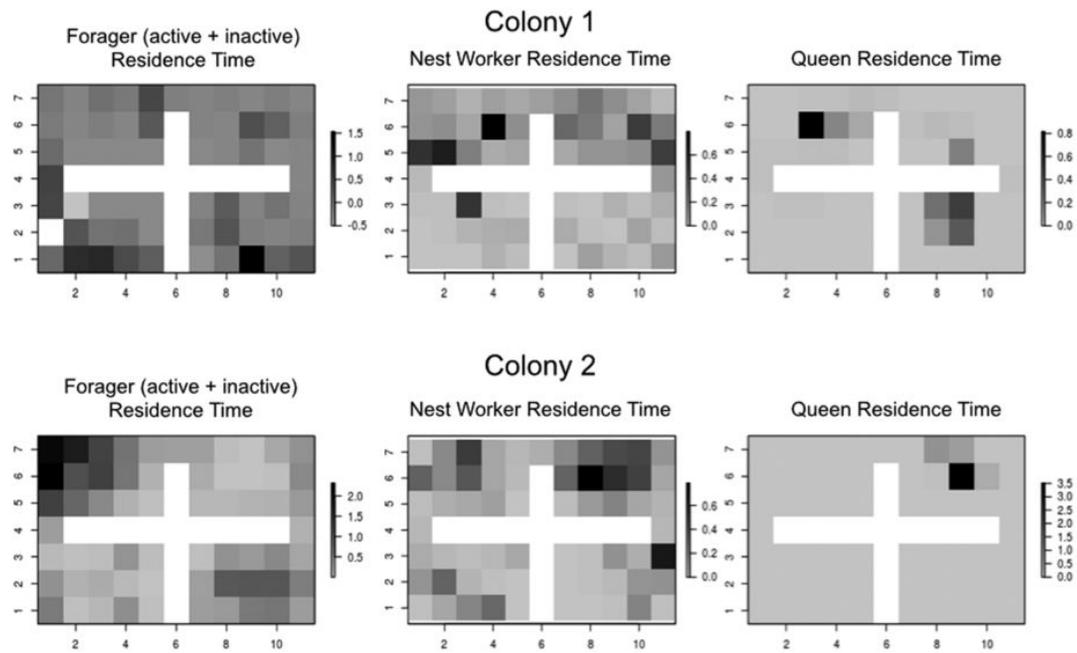
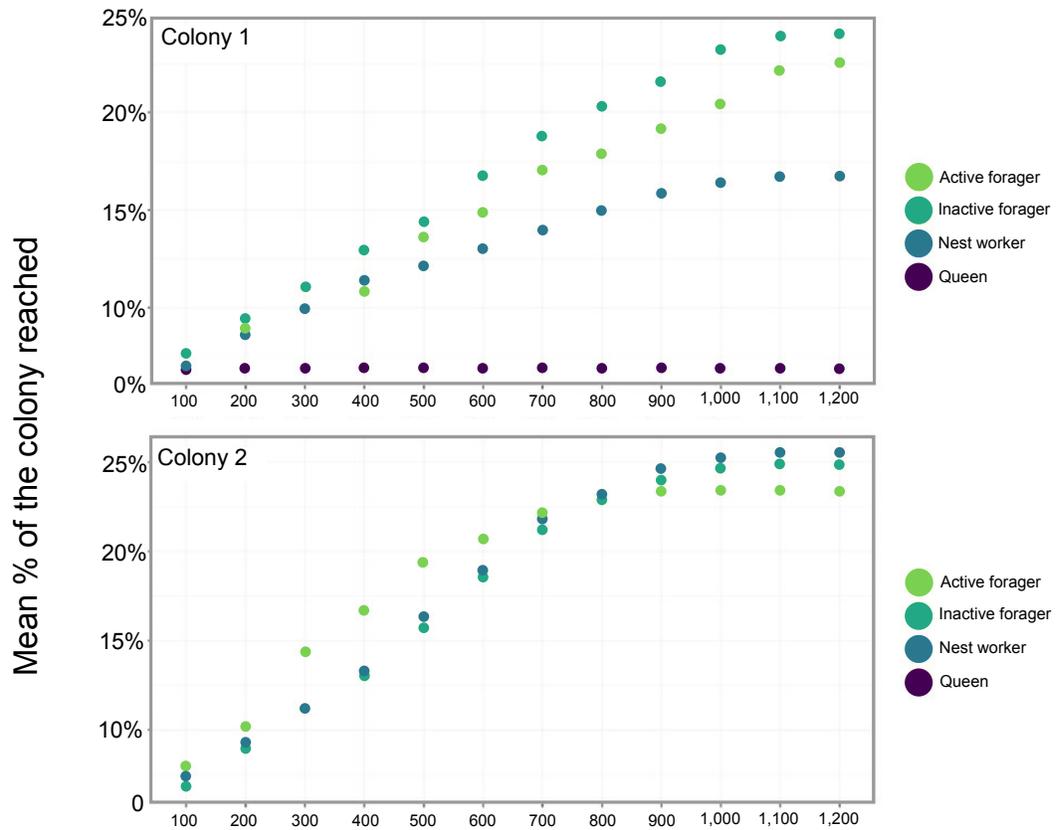


Figure 5.5: Simulated resource spread analysis.

Mean percentage of the network reached over time when a theoretical food source is initiated from a given individual over the observed time ordered networks. Fractions are averaged by behavioral class over all 8 observation nights.



Evidence for organizational immunity via social segregation, but not temporal network structure, in ant trophallaxis networks.

6.1 Abstract

Ant colonies are host to a diverse array of parasitic organisms, and evolving a suite of anti-parasite defenses has likely been crucial to their ecological success. It has been posited that the social and spatial organization of ant colonies may function to prophylactically reduce intra-colonial disease transmission ('organizational immunity'). In this study, we focus on a crucial social interaction, the sharing of liquid food (trophallaxis), and investigate whether ant trophallaxis networks exhibit organizational immunity through the social segregation of potentially infectious individuals (e.g. foragers) and the most important colony member, the queen. Using the carpenter ant *Camponotus pennsylvanicus* as a model system, we investigate whether the temporal structure of ant trophallaxis networks might be protective through either temporal or social filtering processes, or through the diffusive reach of foragers. While we do find evidence of organizational immunity through the direct segregation of foragers and queens, ant trophallaxis networks do not appear to exhibit nuanced organizational immunity in their temporal structure. Colonies need to balance the efficient distribution of food resources with preventing disease spread, and direct social segregation may provide adequate prophylactic protection against the few ant parasites that are capable of *per os* transmission.

6.2 Introduction

A presumed significant cost of social living is the increased burden of infectious disease [73, 74, 78, 492]. The increased density and frequency of potentially infectious contacts contribute to a generally positive correlation between group size and parasite prevalence and infection intensity [1–3, 167] (cf. [87]). To deal with this increased parasite pressure, many group living organisms have evolved defense mechanisms, both physiological and behavioral, to offset these costs [96, 97, 493]. Indeed, the strength of these defenses coupled with the evolution of virulence is such that higher parasite prevalence may indeed select for higher levels of sociality [494].

The ants (Hymenoptera: Formicidae) are host to a wide diversity of parasites [91, 406], but remain one of the most ecologically dominant groups of organisms on Earth [5, 6]. Though little is known about the intensity of the parasite pressure that ants face, their ecological success implies that they effectively manage their disease burden. To accomplish this, ants have a variety of immune defenses, which can be prophylactic, preventing the introduction of infectious parasites into their colonies or inducible, preventing further transmission once a parasite has been successfully introduced (reviewed in Chapter 1). These mechanisms include the suite of traditional immunological responses that insects possess, from encapsulation and melanization to the Spaetzle-Toll, Imd and JAK/STAT pathways (reviewed in [100]). Ants, as social living organisms, also benefit from a suite of socially mediated anti-parasite defenses, collectively termed ‘social immunity’ [97, 99, 128]). These defenses can be physiological or behavioral, including the sharing of immune modulators between nest mates [133], collective disinfection of the nest [146], and social grooming of infectious particles off of nest mates [140].

In addition to these physiological and behavioral immune defenses, it has been posited that ant colonies benefit from additional protection through the spatial and social arrangement of their colonies, termed ‘organizational immunity’ [129]. Proposed mechanisms of organizational immunity include limiting the number of individuals potentially exposed to parasites in the first place and limiting subsequent spatial and social contact between these individuals and unexposed nest mates. Through their efficient division of labor, only some members of ant colonies leave the relatively protected confines of the nest in order to forage, engage in territory defense, and perform external nest maintenance tasks [5]. Since the majority of parasites infecting

ants require encountering potential hosts in the extranidal environment (Chapter 2, Figs. 2.7 and 2.9), it is these ants (hereafter, ‘foragers’) that represent the most likely means of parasite introduction to colonies.

The tasks that foragers and other extranidal workers accomplish are essential to colony functioning, but colonies could minimize potential parasite transmission through the spatial and social segregation of these individuals once they have re-entered the nest [97, 129]. Theoretical studies have shown that spatial structuring alone can help limit the spread of disease [155, 495, 496]. The spatial segregation of foragers has been empirically demonstrated in both ant colonies [152, 449, 473, 477] and bee colonies [153, 475], and modeling studies have shown that the structure of these empirically observed spatial networks can reduce colony-wide transmission [154].

Social segregation has been harder to quantify, as most social insect network studies have made use of proximity or spatial coincidence to infer network connections. It remains unclear whether social organization in social insect colonies promotes the spread of beneficial resources (e.g. information or food) while mitigating the transmission of infectious agents. Blonder et al. (2011) measured the network structure of antennal contacts between ants, an intimate social contact used to transfer information, and found that the network structure optimized fast, local information spread between individuals but resulted in slower spread of information over the entire colony [474]. They hypothesized that this slower spread over the whole colony might function as disease prophylaxis. Richardson et al. (2017) found that ‘burstiness’ within antennal networks, combined with the rapid decay of chemical signals, also resulted in the slow or reduced transmission of information throughout the colony [497]. However, they noted that this result wouldn’t hold true for infectious agents that had longer periods of infectivity.

Recently, Gernat et al. (2018) analyzed food-sharing (trophallaxis) networks in bees and found that these networks were characterized by burstiness that accelerated simulated spreading processes [498]. Of all the tasks that ant colonies must accomplish, food acquisition and its subsequent distribution are among the most critical [5]. Foraging ants leave the nest to gather resources, which are brought back and distributed to all members of the colony through the social transfer of liquid food (trophallaxis). However, ants are host to some parasites that require either close proximity or *per os* (oral) transmission, both of which are enabled by the intimate interaction of trophallaxis (e.g. viruses, cestode proglottids, generalist fungi). As such, trophallaxis networks

may be conduits for both positive resources and infectious agents, and the structure of these networks might represent a compromise between the efficient and speedy flow of food while minimizing the risk of intra-colony disease transmission.

The spreading of beneficial resources to all colony members is necessary for colony functioning, so ant colonies have limited options for minimizing parasite transmission via the oral route. The first way that colonies could protect themselves is to socially segregate incoming, potentially infectious foragers from important colony members (i.e. the queen) by limiting direct trophallaxis between them. However, the lack of direct interaction does not preclude the possibility that infectious agents could still be passed down through temporal network connections. Thus, colonies might employ additional filtering mechanisms to limit the spread of potentially infectious food throughout the colony. These filters could be either temporal or social, and would serve to reduce potentially infectious doses arriving to the queen. In the case of ‘temporal filtering’, resources spread from potentially infectious foragers might take longer to arrive to important colony members (e.g. the queen), which could reduce the infectiousness of any dose that those recipients receive (Fig. 6.1a). With ‘social filtering’, resources spread from potentially infectious individuals (e.g. foragers) might have to go through more social partners before they are able to reach the queen, with each additional partner serving as an additional layer of filtering (Fig. 6.1b).

In this work, we test if an ant social network has organizational immunity through social segregation, temporal filtering, or social filtering. We use the black carpenter ant, *Camponotus pennsylvanicus*, which is a typical ant species with medium-sized colonies (5 - 15,000 ants) and no strong physical differences in caste between workers. First we look for evidence of social segregation by observing whether foragers avoid direct trophallaxis interactions with the queen. Next, we look for how these potentially infectious foragers are temporally connected to the queen through their mutual connections by analyzing the minimum time (temporal filtering) and minimum number of individuals (social filtering) it would take resources spread from foragers to reach the queen. We then investigate how temporal network structure impacts diffuse resource spread within colonies by looking at the number of temporal partners that ants have. Finally, we simulate the spread of resources with varying decay periods and measure how long it takes to reach specified levels of colony saturation. Collectively, this work asks whether signatures of organizational immunity are prophylactically present in carpenter ant societies via the structuring of their trophallaxis networks.

6.3 Methods

Colony set-up and filming

Colony collection, nest set-up, and filming were performed by Andreas Modlmeier and methods are described in Modlmeier et al. (*in prep*). Three queen-right colonies of the black carpenter ant, *Camponotus pennsylvanicus*, were collected in Centre County, Pennsylvania, U.S.A. in spring 2015. One week prior to filming, a queen, 85 workers, and 15 larvae were selected to form each colony. Ants were individually labeled by affixing QR labels to their thoraxes with glue [499].

To mimic the natural conditions in which *C. pennsylvanicus* colonies live, ant colonies were individually housed in wooden nests contained within filming boxes. Nests contained interior walls in order to mimic chambers and these nests were connected to an outside foraging arena where ants had *ad libitum* access to food (20% sucrose solution, cricket protein source) and water. Inside the filming boxes, nests were illuminated with infrared (IR) lights while maintaining complete darkness for the ants (who cannot perceive IR light). Modified GoPro Hero3/Hero3+ cameras that could film under IR lighting conditions were mounted to the tops of the filming boxes. Colonies were allowed to habituate for a week before they were filmed for a period of four hours. Following filming, nests were modified to give them extra space, colonies were allowed to re-habituate for a week, and were then filmed for an additional four-hour period. Modlmeier et al. (*in prep*) found no difference in overall social network metrics between these high- and low-density treatments, so we do not distinguish between them for our analyses below.

Ant trophallaxis networks and assigning behavioral roles

For each colony, the trophallaxis network for two 4-hour filming periods were scored by Modlmeier et al. (*in prep*) using the same methods as described in Chapter 5. The identities of the interacting ants, as well as the start time, stop time, and location (chamber) of their interaction was recorded.

In addition to their trophallaxis interactions, ants were scored for their behavioral roles within the nest. Ants that left the nest during the observed filming period were scored as foragers, ants that were never observed to leave the nest were scored as nest workers, and individuals that interacted directly with the queen were scored as retinue

workers.

Static network measures

The static network metrics of degree and betweenness centrality were calculated in R [457] using the ‘igraph’ package [480]; additional details are described in Chapter 5. To test whether there were statistically significant differences in network metrics between ant types, Kruskal-Wallis tests were performed. Dunn tests with a Benjamini-Hochberg correction for multiplicity of hypothesis testing were then used to determine pair-wise comparisons between ant behavioral types.

Temporal network measures

We calculated the shortest time paths and shortest social paths from all individuals to the queen for all three colonies. In addition, we calculated the number of unique first, second, and third-order partners for each ant.

We calculate the shortest time paths and shortest social paths between individuals using the ‘shortesttimepath’ and ‘shortesthoppath’ functions from the package ‘timeordered’ [500] in R [457]. The shortest time path is the minimum amount of time it would take from when an individual first participates in any trophallaxis event in the network to when resources spread through that initial interaction could reach the queen. The shortest social path (number of ‘hops’) is the minimum number of unique individuals that resources spread from a starting interaction would have to go through in order to subsequently reach the queen (not including the starting individual or the queen). For some individuals, such as retinue workers that directly interact with the queen, there isn’t any social filtering. For other individuals, there aren’t any causally permitted paths in the network that would allow for resources to spread to the queen.

To find the number of first-order partners for a given focal ant, we simply identify all of the unique individuals that they exchange food with directly. To find second-order partners, we determine all of the unique future partners that the focal ant’s first-order partners interacted with after they had interacted with the focal ant. To find third-order partners, we find all of the unique future partners that the focal ant’s second-order partners interacted with after they had interacted with the first-order partners (Fig. 6.2). Occasionally, ants could be partners of multiple orders (i.e. both a first-order partner and second-order partner); in this case, we counted them according

to their lowest order of association with the focal ant. Since the number of temporal partners observed is limited by the temporal observation period (here, four hours = 14,400s), we limited our calculations of first-, second-, and third-order partners by only counting partners which stemmed from interactions that happened within the first hour of filming.

Simulated resource spread

To understand whether organizational immunity might be discernible in how resources are distributed throughout the entire colony and not just to the queen, we simulated resource spread through the empirically observed networks. To accomplish this, we designate a single ‘seed’ individual at time $t = 0s$ as having food that will decay in a step-wise manner after a set decay period (decay periods = 15, 30, 60, and 90 minutes). This seed individual then interacts with other ants as was observed in the empirical networks; if an interaction takes place before the decay time has been reached, then the interacting partner becomes ‘fed’ and is capable of spreading the resource to others through their future interactions. Thus, the resource is capable of spreading temporally through the seed ant’s partners, partners’ partners, and so on. Once the decay period has expired for an individual, they are no longer ‘infectious’, but can become fed by others and thus can become ‘infectious’ again.

We make the assumption that any interaction with the seed ant within the decay time window will result in the perfect transfer of the resource and that each ant that subsequently becomes fed is able to spread the resource with the same set decay period (e.g. each ant has 30 minutes from when they were first fed to spread the resource). We further assume that the decay period of the donor ant is unaffected by these interactions (i.e. spreading the resource does not speed up resource decay).

Resource spread simulations were performed in R using bespoke code. Every ant in all colonies was used as the seed ant for a single simulation per network observation and per decay period and only one ant was seeded with food per simulation. Since many individuals might be able to diffuse food throughout the colony using their network interactions, we were interested if certain ant behavioral types might be faster or slower at this diffusion process. For every simulation, we calculated the minimum amount of time it would take to diffuse food to 10%, 25%, 50% and 75% of the colony when food decay periods were 15, 30, 60, and 90 minutes.

6.4 Results

We are interested in assessing whether carpenter ant colonies employ organizational immunity in their trophallaxis networks via social segregation or through nuanced temporal network structure. Below, we describe results for whether foragers and queens are socially segregated and for whether their trophallaxis networks show evidence of temporal or social filtering. Additionally, we compare the diffusive reach of foragers versus other ant behavioral classes.

Dyadic interactions

Foragers and queens never directly exchanged food in any of the 24 hours of video observed (3 colonies x 4 hours/night x 2 filming nights), though foragers did exchange food with retinue workers (Fig. 6.3a). The most common interaction dyad was between nest workers (NN, 60.97% of interactions), followed by nest worker - retinue (NR, 19.22% of interactions), and forager - nest worker (FN, 11.02% of interactions) (Fig. 6.3a).

To understand whether the observed dyadic interaction patterns are due to social structuring within colonies or simply due to differences in the numbers of individuals in each behavioral class, we randomized networks by maintaining the number and time stamps of interactions but allowing social partners to vary randomly. For each randomization, all ants were assumed to have equal probability of being in a given interaction. For each empirical network, we randomized the edge list 1,000 times using the 'totalrandomization' function from the 'timeordered' package in R [457,500], resulting in 3,279,528 interactions in 6,000 randomized networks (Fig. 6.3b). The mean and standard deviation of the percentage of interactions in each dyad type are given in Fig. 6.3b. In these randomized networks, foragers and queens did interact with each other, though this accounted for a very low percentage of the total number of interactions (0.11%). The distribution of dyadic interactions in the empirical and socially randomized networks appear to be qualitatively the same, suggesting that the patterns of interaction in ant colonies may be the result of the number of individuals in each behavioral class, rather than social structuring on the part of the ants.

Static network analysis

We first analyzed holistic differences in the static network metrics between ant behavioral classes to determine if ant types were behaving differently from one another. Mean static network metrics across ant types for colonies 1-3 (degree and betweenness centrality) are given in Table E.1. Statistical results (χ^2 values, degrees of freedom, and p-values) from the Kruskal-Wallis and Dunn tests are reported in Table E.2. Forager ants participated in a higher number of trophallaxis events (mean = 38.6, 27.25, and 16 interactions for colonies 1-3, respectively) over the 4-hour observation period than nest workers, retinue workers, or queens, but differences between groups were not statistically significant except in colony 3 (Table E.2). In colony 3, retinue workers had a significantly higher degree centrality than their nest worker counterparts (Dunn test, $p=0.0031$).

Betweenness centrality was highest amongst the retinue workers and the queen (Table E.1), though this difference was not statistically significant except in colony 3 (Table E.2). In colony 3, retinue workers had a significantly higher betweenness centrality than nest workers (Dunn test, $p = 0.0007$).

Temporal network analysis: temporal filtering

Though no real differences were detected in the static network metrics of each ant type, the temporal network metrics of each ant type could nevertheless be distinct. The mean minimum times to reach the queen as a function of ant behavioral type are given in Table 6.1a and shown in Fig. 6.4. The minimum times it took from an ant's first interaction to being able to reach the queen via network interactions ranged from 0s (if the first interaction an ant had was with the queen) to 12,151 seconds (Fig. 6.4). In colonies 1 and 2, there was a significant difference in the minimum time it took to reach the queen between foragers and retinue workers and nest workers and retinue workers (Table 6.2a), with retinue workers having a faster minimum time to reach the queen. In colony 3, there was only a significant difference in the minimum time to reach the queen between retinue workers and nest workers (Table 6.1).

Temporal network analysis: social filtering

The mean number of individuals in the temporal network paths between a focal individual and the queen ('hops') are given in Table 6.1b and shown in Fig. 6.5. By definition, retinue workers are workers that had direct trophallaxis interactions with the queen, so the minimum number of hops between them and the queen is always zero. For nest workers and foragers, the number of hops in the transmission chain to the queen ranged from 1 to 7 individuals. In all colonies, there were statistically significant differences in the number of hops between retinue workers and foragers as well as retinue workers and nest workers (Table 6.2b), but there was no statistically significant difference in the minimum number of hops between foragers and nest workers except in colony 2 (Fig. 6.5).

Temporal network analysis: n. of time-ordered partners

The number of second-order partners ranged from 0 - 35 unique individuals, with a mean of 12.44 averaged over all colonies (Fig. 6.6). The number of third-order partners ranged from 0 - 29 unique individuals, with a mean of 8.013 averaged over all colonies (Fig. 6.6). There was no significant difference in the number of either second- or third-order partners between ant behavioral types (Tables 6.3, 6.4).

Simulated resource spread

An example output plot of simulated resource spread through a colony is shown in Fig. 6.7. We report the mean and standard deviation of minimum times to reach 10%, 25%, 50% or 75% colony saturation in Table 6.5 and show violin plots of the distribution of minimum times to reach a certain saturation threshold as a function of food decay period in Fig. 6.8. On average, it always took longer periods of time to reach higher percentages of colony saturation (Table 6.5, Fig. 6.8). Furthermore, as the length of the decay period increased (i.e. individuals remained capable of spreading food for a longer duration of time), the minimum time to reach the different colony saturation thresholds decreased (Table 6.5, Fig. 6.8). In order to reach 75% colony saturation, food decay periods had to be either 60 or 90 minutes, and to reach 50% colony saturation, food decay periods had to be 30 minutes or longer (Table 6.5). There was no significant difference in the minimum times to reach 10%, 25%, 50% or 75% colony saturation

between ant behavioral types for any of the decay periods used (Table 6.6, Figs. E.2 - E.5.). Resources seeded from any behavioral type were able to reach colony saturation thresholds in approximately the same minimum amount of time.

6.5 Discussion

Foraging ants represent a double-edged sword for ant colonies; they bring in necessary food resources but also act as potential conduits for parasite entry and further transmission between nest mates. In this study we investigated whether organizational immunity was present in the trophallaxis (food-sharing) networks of the carpenter ant, *C. pennsylvanicus*.

We found evidence that foragers are socially segregated from the most important colony member, the queen. Foragers and queens never directly exchanged food in any of the 24 hours of observation (Fig. 6.3), which confirms results found in previous studies [449]. This lack of direct contact is important in two ways. Firstly, it forces food being delivered to the queen to have to go through at least one intermediate partner (social filtering), and secondly, by not engaging in trophallaxis together, foragers and queens likely do not have prolonged physical contact, thus preventing the spread of infectious material via direct physical contact. Though this study did not look at spatial co-occurrence by ant behavioral types within the nest, previous work has shown that foragers do occupy different areas of the nest [152, 449], and that when foragers are in the same chamber as the queen, they may speed their movement [449]. The mechanism behind the social segregation of foragers and queens remains unknown. It could be that foragers and queens do not spatially overlap enough to engage in trophallaxis, or that the relatively small numbers in each of these behavioral types means that even under random mixing their interactions would be infrequent. Our analysis of interaction dyads (Fig. 6.3) shows that the distribution of dyadic interactions in the empirical and socially randomized networks appear to be qualitatively the same, suggesting that the patterns of interaction in ant colonies may be the result of the number of individuals in each behavioral class, rather than social structuring on the part of the ants. Ants could also be truly behaviorally avoiding one another, using differences in cuticular hydrocarbons to tell nest mates apart [501]. Future empirical studies are needed to tease this apart and to assess whether the direct social segregation of foragers and queens observed here is protective when infectious agents

are explicitly introduced.

While foragers and queens never directly interact, infectious agents are still capable of transmitting from foragers to the queen through the temporal structure of ant trophallaxis networks. We assessed whether ant trophallaxis networks might employ more nuanced forms of organizational immunity in the form of temporal or social filtering (Fig. 6.1). When we compared the minimum amount of time it takes from an individual first participating in the trophallaxis network to when they could temporally reach the queen, we found no significant difference between ant behavioral types (Fig. 6.4, Tables 6.1a, 6.2a). Furthermore, when we compared the minimum number of intermediate individuals (hops) between a given focal ant and the queen, we found no significant difference between foragers and nest workers (Fig. 6.5, Tables 6.1b, 6.2b). Thus, while social filtering is in place due to the fact that foragers never directly interact with the queen, the functional outcome of their temporal network structure isn't different from that of nest workers.

To further examine whether the temporal trophallaxis network structure of foragers might be different than that of other ant behavioral types, we calculated the number of time-ordered partners (second-order and third-order) as a function of ant behavioral type (Fig. 6.6, Table 6.3). We found no significant differences in the number of either second- or third-order partners between ant behavioral types, suggesting that foragers do not have a smaller or larger diffusive reach within the colony. Additionally, our analysis of theoretical food diffusion through the empirical temporal networks showed that there was no difference between ant behavioral types in the minimum time it would take food seeded from one individual to reach various percentages of the colony. While nest or retinue workers aren't bringing in resources for distribution, this analysis shows that the temporal networks of foragers are not privileged in such a way as to limit the spread of their food throughout the colony in a timely manner. Our spread analysis was conducted with the assumption that only one individual was seeded with food at the beginning of our simulations, but natural colonies, especially large ones, have many incoming foragers distributing food simultaneously. Thus, colonies likely become saturated at higher percentages more quickly than what our analysis here predicts. Indeed, studies that have followed food distribution within colonies have found that ant colonies can become rapidly saturated (within 30 minutes) [477, 502].

While it appears that ant trophallaxis networks do not employ nuanced mechanisms of organizational immunity except for the direct segregation of foragers and

queens as prophylactic defense, an interesting area of future investigation is whether trophallaxis networks could become altered in the presence of parasites. Several studies have shown that individual ants infected with generalist fungi alter their behavior by engaging in fewer social interactions [143, 503]. Other studies have shown that ants exposed to a non-lethal immune challenge increased the amount of trophallaxis that they participated in [130, 131]. Such behavioral alterations at the individual-level could cascade up to alter network topology. Thus, while the trophallaxis networks of social insects seemed to be optimized for the rapid distribution of food [477, 498, 502], trophallaxis network structure could potentially dynamically re-assort based on individual infection status. Recent advances have made the simultaneous tracking of trophallaxis interactions and food flow possible [504], and this methodology offers a promising tool for investigating the dynamical re-assortment of trophallaxis networks and the impact of these re-assortments on colony food distribution.

In summary, this study provides evidence to support the claim that ant colonies have prophylactic organizational immunity in their trophallaxis networks. Foragers and the queen are socially segregated from one another, which likely protects against parasites that transmit either *per os* or through direct contact. We do not find evidence of more nuanced forms of organizational immunity in the temporal structure of the trophallaxis networks- either in temporal or social filtering with respect to the queen, the number of time-ordered partners, or in the diffusion of resources through the entire colony. Though foragers do employ some degree of social filtering because food originating from them has to go through intermediates to reach the queen, their temporal network measures are not different from those of their nest mate counterparts.

Colonies need to balance the fast and efficient distribution of resources to all members of the colony with the mitigation of potential disease transmission. Given that known ant parasites that transmit via trophallaxis are relatively scarce [?, 91], and both solitary and social insects have a suite of individual immune defenses in order to contend with infectious agents that may be in their food (reviewed in [100]), it seems unlikely that ant trophallaxis networks are temporally optimized for the reduction of potential parasite transmission. Simply avoiding direct interactions between foragers and the queen likely provides sufficient protection, though future empirical studies explicitly incorporating infectious agents are needed to assess whether this is indeed the case.

Acknowledgements

I would like to thank Andreas Modlmeier for supplying the empirical network data used in this study, as well as the many undergraduate research assistants who scored the trophallaxis interactions between ants that made up this data set. This work was funded by a NSF Graduate Research Fellowship under Grant No. DGE1255832 to LEQ and NSF Grant No. 1414296 to DPH as part of the joint NSF-NIH-USDA Ecology and Evolution of Infectious Diseases program.

6.6 Figures and Tables

Figure 6.1: Temporal and social filtering.

Schema for how temporal and social filtering could serve as mechanisms of organizational immunity inside ant colonies. (a) In temporal filtering, the time delay between a potentially infectious individual interacting with an important colony member (i.e. the queen) could reduce disease transmission if infectiousness decays over time. (b) In social filtering, the serial passage of potentially infectious resources could dilute the infectious dose given to important colony members.

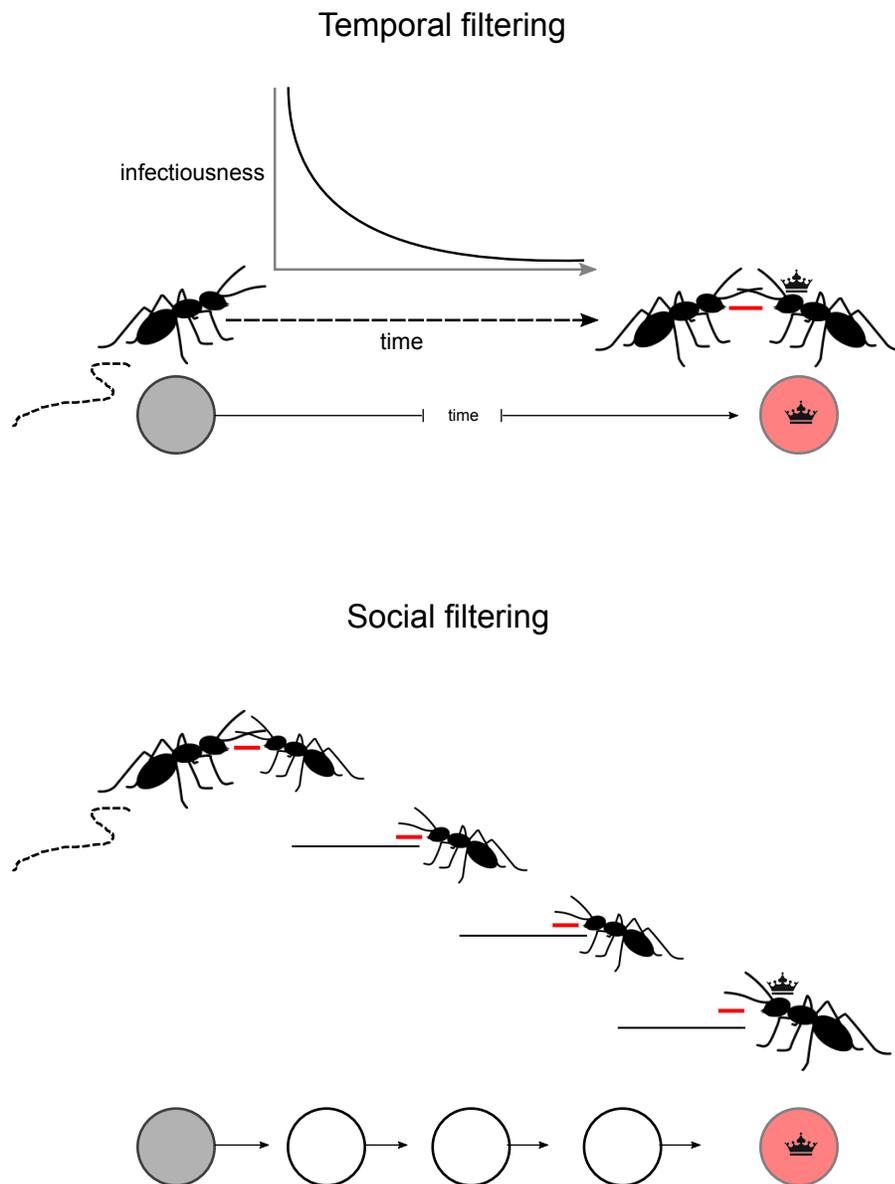


Figure 6.2: Time-ordered partners in ant temporal networks.

Time-ordered interactions and partners in ant colonies. When the timing of interactions is considered, focal individuals (purple horizontal line) can have a potentially large transmission potential because they can pass along resources to their partners ('first-order' partners, blue horizontal lines), and these partners can in turn spread the resources to their partners' partners ('second-order' partners, green horizontal lines). If resources last long enough, they can continue to be passed forward in time, potentially reaching third-order partners (light green horizontal line).

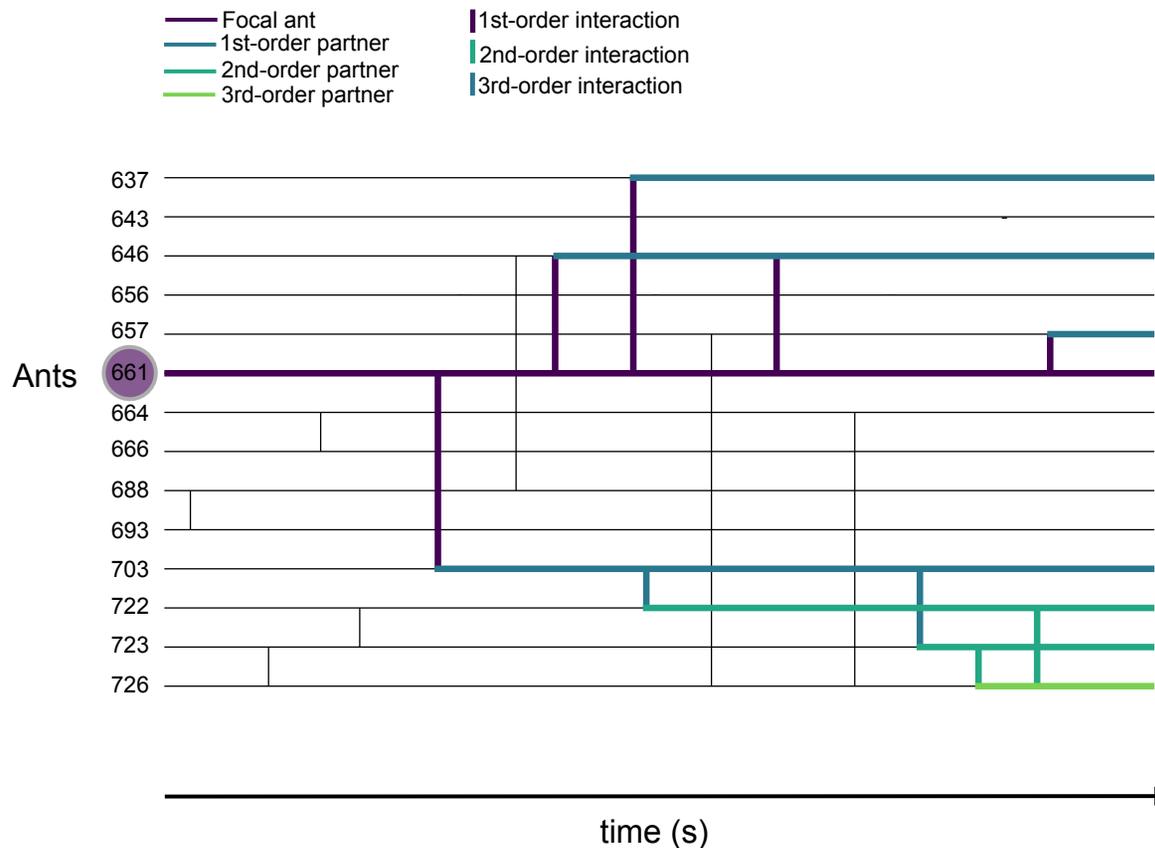


Figure 6.3: Dyadic interactions between ant behavioral types.

(a) Bar plots of the mean percentage of interactions of a certain dyad type summed across all colonies and nights of observation (n = 6 networks). Dyad types are: FF forager-forager, FN forager- nest worker, FR forager-retinue, NN nest worker-nest worker, NR nest worker-retinue, QR queen-retinue, and RR retinue-retinue. Error bars represent \pm standard deviation. No interactions were ever observed between foragers and queens. (b) Bar plots of the mean percentage of interactions of a certain dyad type for networks in which interactions were randomized between ants. Ants had equal probability of participating in a given interaction; the time stamps of interaction and total number of interactions were preserved, only ant identities were randomized. 1,000 randomizations were performed per colony-night (n = 6,000 networks).

Empirical and randomized trophallaxis dyadic associations

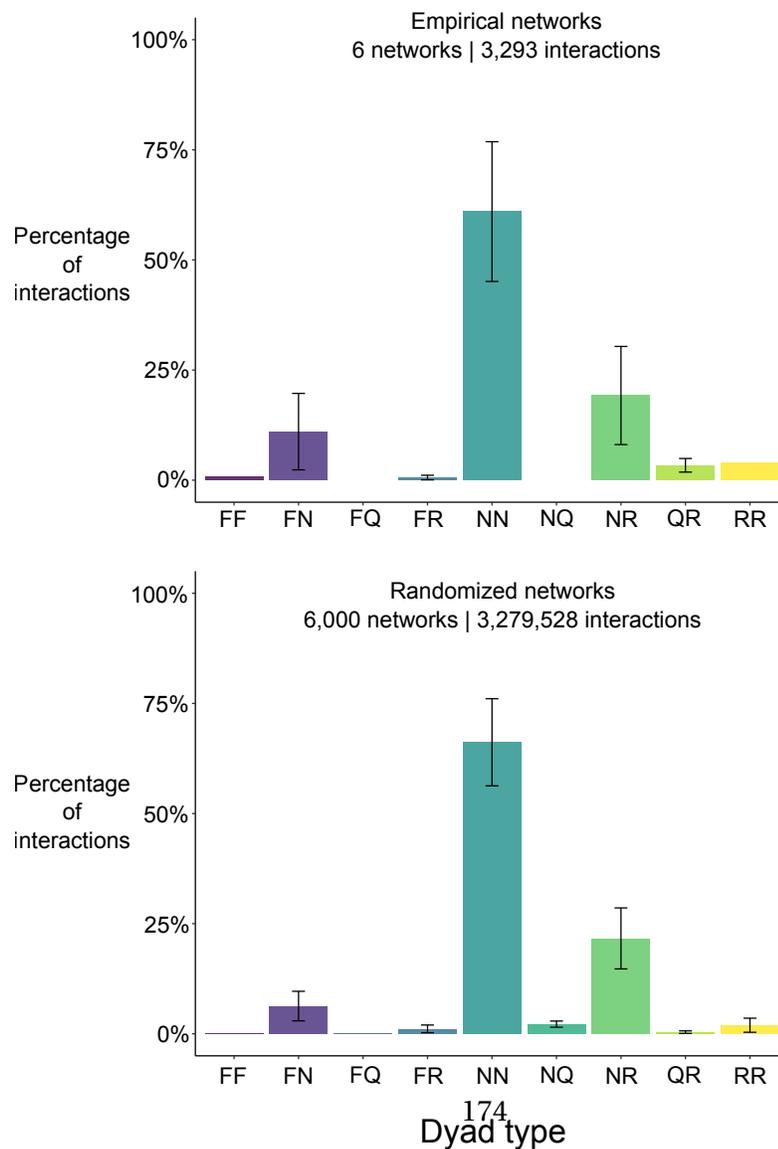


Figure 6.4: Minimum times to reach the queen

Violin plots showing the minimum times to reach the queen as a function of ant behavioral type for colonies 1-3. Black circles represent the median values of minimum time, asterisks represent statistically significant post-hoc Dunn tests on differences between ant behavioral groups.

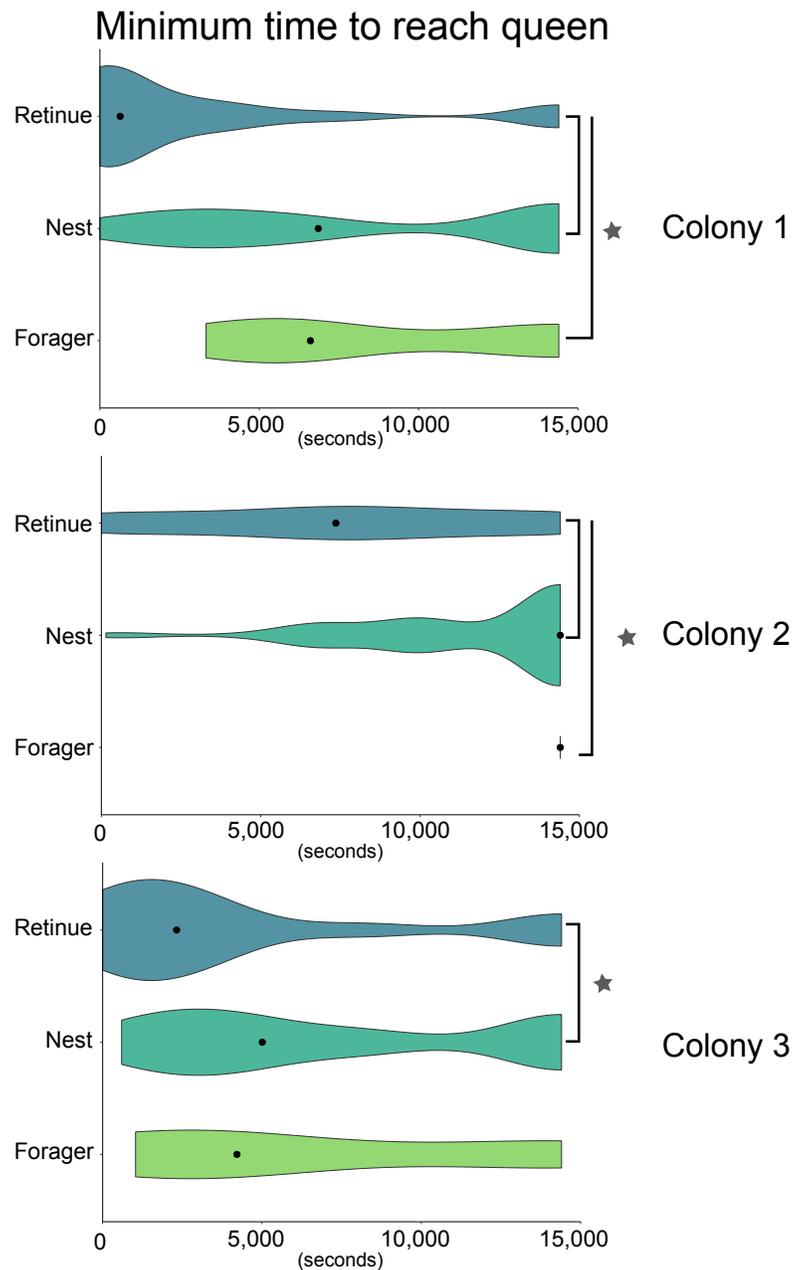


Figure 6.5: Minimum hops to reach the queen.

Violin plots showing the minimum number of hops (intermediate ants) needed for an individual to reach the queen through temporal network paths as a function of ant behavioral type for colonies 1-3. Black circles represent the median values of minimum number of hops, asterisks represent statistically significant post-hoc Dunn tests on differences between ant behavioral groups.

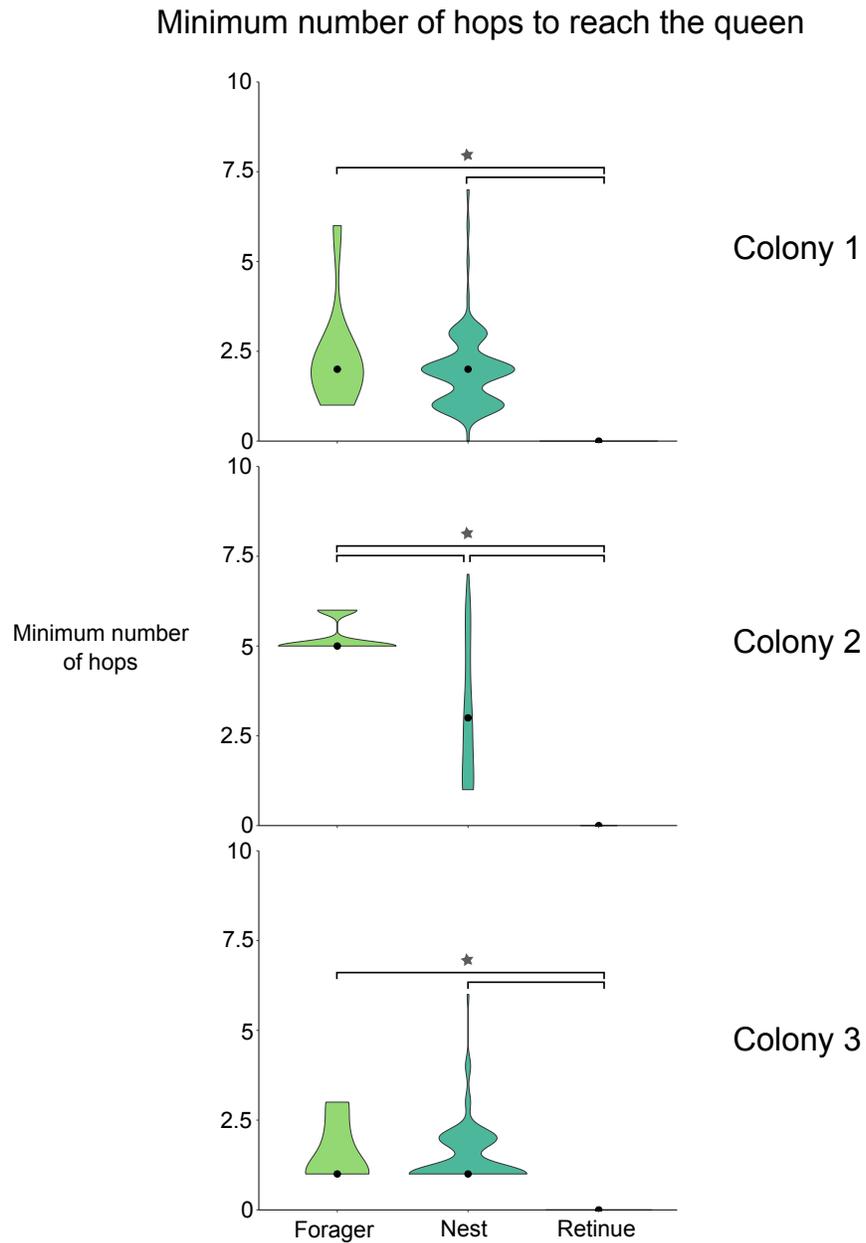


Figure 6.6: Temporal network metrics.

Temporal network metrics (n. of second- and third-order partners) as a function of ant behavioral group for colonies 1- 3. Solid black lines represent the median values, boxes represent data within the 25th - 75th percentiles, and whiskers extend to 1.5 times the interquartile range. Asterisks represent statistically significant differences between groups using Kruskal-Wallis tests (see Table 6.4).

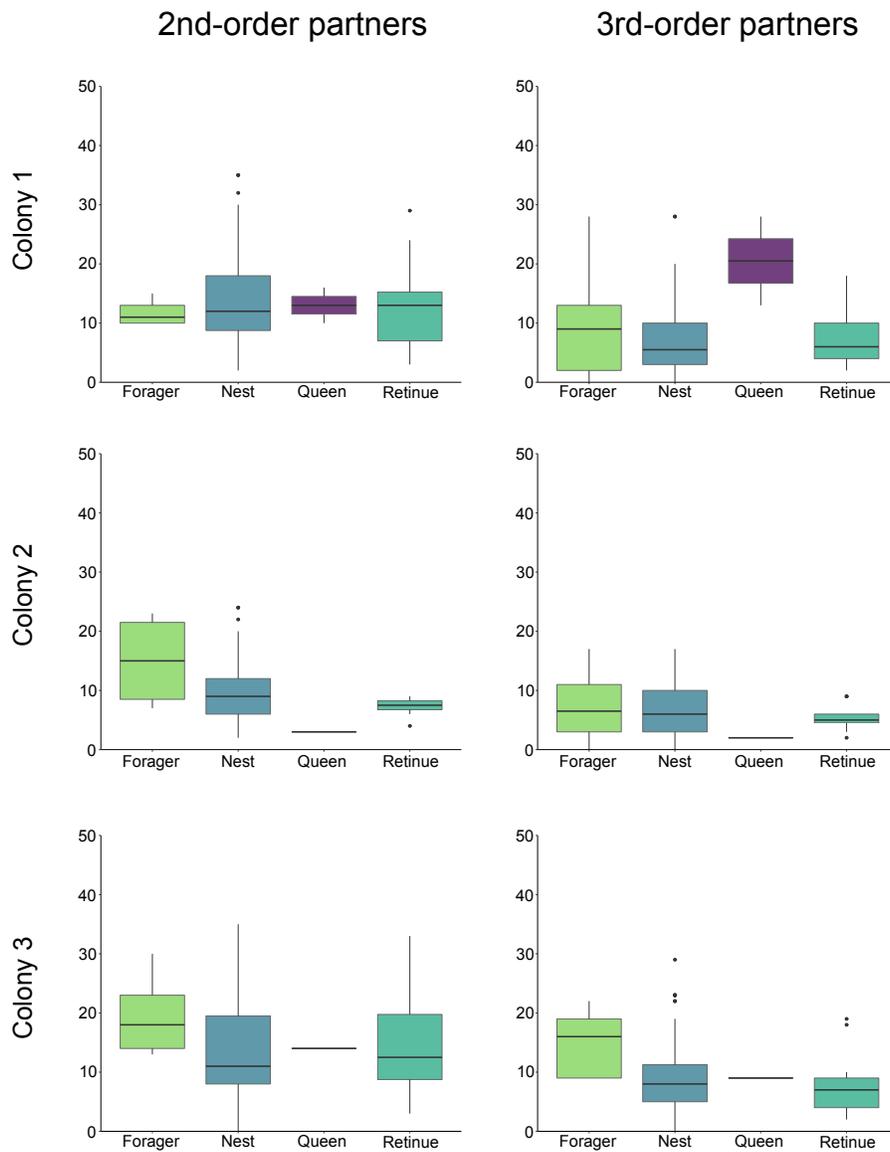


Figure 6.7: Simulated resource spread through temporal networks by ant behavioral type.

An example output plot of simulated resource spread through the empirically observed temporal networks. Each line represents a single simulation in which one individual had food at time $t=0$ s and subsequently spread that food through its temporal network partners. For each simulation, we calculated the minimum time needed to saturate 10%, 25%, 50%, and 75% of the colony with food.

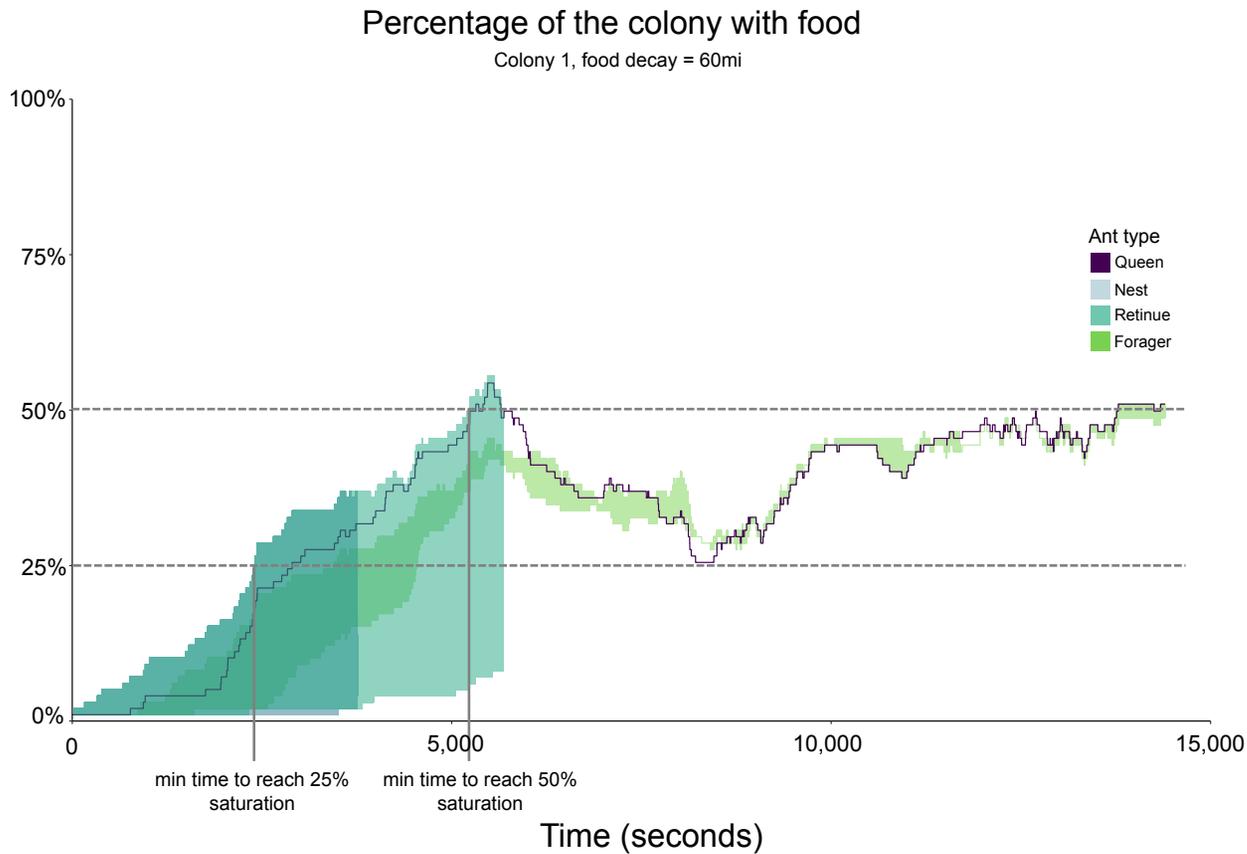


Figure 6.8: Time to colony saturation as a function of food decay period.

Violin plots showing the distributions of minimum time needed to reach 10%, 25%, 50%, or 75% colony saturation with food as a function of the food decay period for all colonies combined together. Black circles represent the median values of minimum time to reach the saturation threshold.

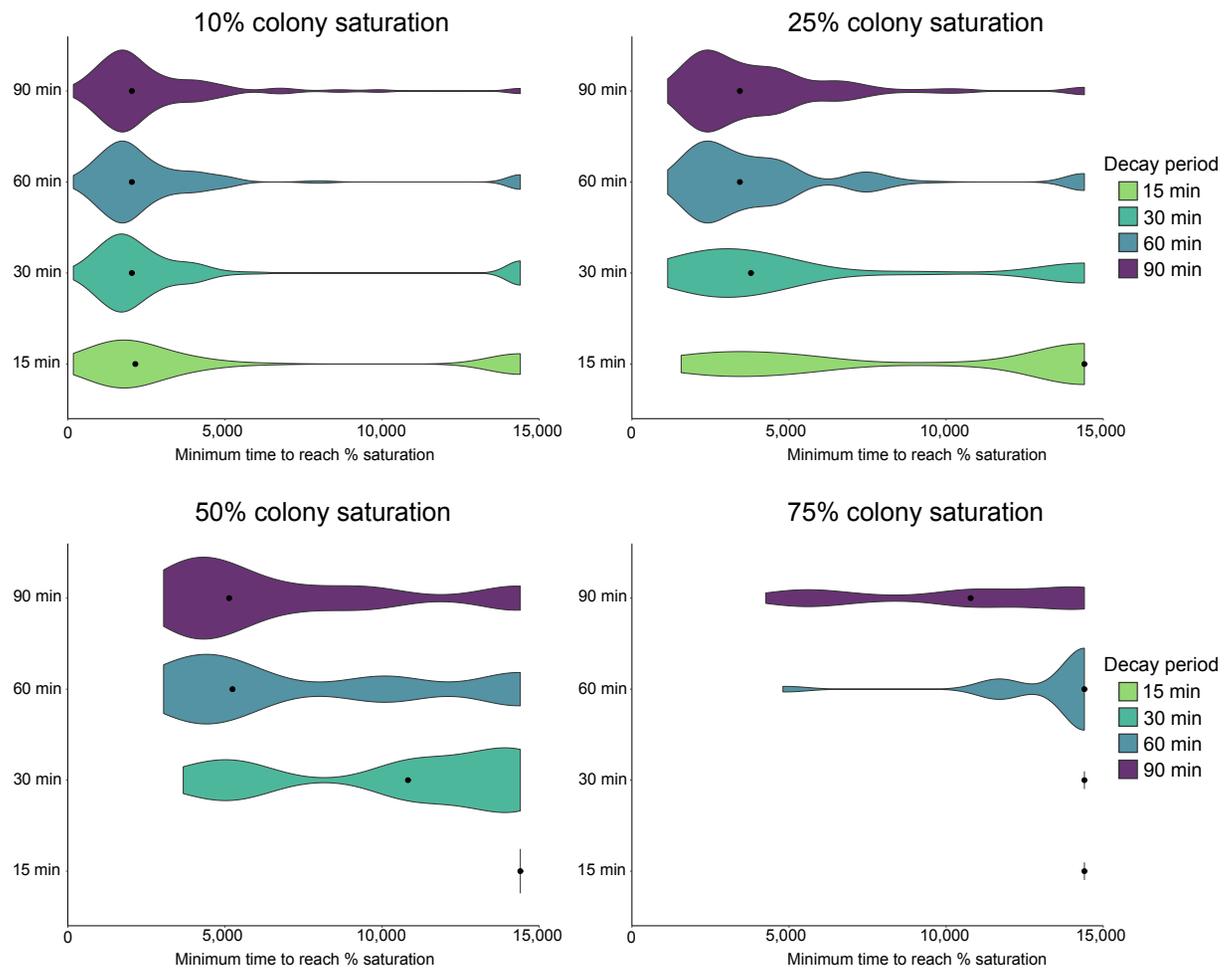


Table 6.1: Minimum time and number of individuals in transmission chains to the queen.

Mean (a) minimum times and (b) minimum number of individuals in transmission chains to queens for colonies 1-3. If a transmission chain originating from an individual never reached the queen, then the min time was set to the max observation time (14,400s), and that individual was excluded from the analysis in (b).

a. Mean minimum time to reach the queen			
	Colony 1	Colony 2	Colony 3
Forager	8996.1 (10)	14400 (5)	6573.5 (6)
Nest	8402.621 (116)	11802.94 (132)	7428.74 (124)
Retinue	3224.273 (22)	7560 (12)	4504 (27)
b. Mean minimum n. individuals in chain to reach the queen			
Forager	2.375	5.25	1.6
Nest	1.96	2.98	1.49
Retinue	0	0	0

Table 6.2: Statistical results for minimum time and number of individuals in transmission chains to queens.

Kruskal-Wallis χ^2 , degrees of freedom, and p-values for (a) differences in the minimum time for a seed ant to reach the Queen and (b) minimum number of unique individuals in the transmission chain between a seed ant and the queen as a function of ant behavioral role (ant type). If a transmission chain originating from an individual never reached the queen, then the min time was set to the max observation time (14,400s), and that individual was excluded from the analysis in (b). Asterisks represent statistically significant differences between groups at $\alpha = 0.05$ level. (c) Significant results from a post-hoc Dunn test for pairwise comparisons in min times and min hops between groups.

Statistical test results			
a. Minimum time to reach queen			
	χ^2	df	<i>p-value</i>
Colony 1	21.467	2	<0.001*
Colony 2	12.055	2	0.002*
Colony 3	10.937	2	0.004*
b. Minimum n. individuals in chain to reach the Queen			
Colony 1	58.648	2	<0.001*
Colony 2	37.83	3	<0.002*
Colony 3	76.886	4	<0.003*
c. Dunn test results			
	Metric	Comparison	<i>p-value</i>
Colony 1	Time	Retinue-Nest	<0.001
Colony 1	Time	Retinue-Forager	<0.001
Colony 2	Time	Retinue-Nest	<0.001
Colony 2	Time	Retinue-Forager	<0.001
Colony 1	Time	Retinue-Nest	0.0011
Colony 1	Hops	Retinue-Nest	<0.001
Colony 1	Hops	Retinue-Forager	<0.001
Colony 2	Hops	Retinue-Nest	<0.001
Colony 2	Hops	Retinue-Forager	<0.001
Colony 2	Hops	Forager-Nest	0.0182
Colony 3	Hops	Retinue-Nest	<0.001
Colony 3	Hops	Retinue-Forager	<0.001

Table 6.3: Temporal network metrics.

Mean temporal network metrics (number of 2nd-, and 3rd-order partners) by ant type for colonies 1-3.

Mean temporal network metrics						
	Colony 1		Colony 2		Colony 3	
	2nd-order	3rd-order	2nd-order	3rd-order	2nd-order	3rd-order
Forager	11.8	10.4	15	7.5	19.6	15
Nest	13.5	7.26	9.44	6.89	13.59	9.43
Retinue	12.75	7.56	7.25	5.375	14.9	7.25
Queen	13	20.5	3	2	14	9

Table 6.4: Statistical results for temporal network metrics.

Kruskal-Wallis χ^2 , degrees of freedom, and p-values for differences in (a) number of 2nd-order and (b) 3rd-order partners by ant type. Asterisks represent statistically significant differences between groups at $\alpha = 0.05$ level.

Kruskal-Wallis results			
a. Number of 2nd-order partners			
	χ^2	df	<i>p-value</i>
Colony 1	0.092	3	0.99
Colony 2	5.83	3	0.12
Colony 3	4.22	3	0.24
b. Number of 3rd-order partners			
Colony 1	3.47	3	0.32
Colony 2	4.19	3	0.24
Colony 3	2.04	3	0.56

Table 6.5: Mean minimum times to reach certain colony saturation percentages as a function of food decay period.

Mean and st. deviation of the minimum times for a seed ant to reach 10%, 25%, 50%, and 75% colony saturation when decay periods are (a) 15 minutes, (b) 30 minutes, (c) 60 minutes, and (d) 90 minutes.

Simulated resource spread								
a. 15 minute decay period								
	10%		25%		50%		75%	
	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
colony 1	4828.8	5271.7	10049.7	4961.5	14400	0	14400	0
colony 2	9705	6131.7	14400	0	14400	0	14400	0
colony 3	3050.7	3407.7	6805.2	5230.3	14400	0	14400	0
b. 30 minute decay period								
	10%		25%		50%		75%	
	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
colony 1	2945.8	3247.8	4576.3	3385.3	9818.5	4076.9	14400	0
colony 2	6710.9	6053.1	13435.3	3233.5	14400	0	14400	0
colony 3	2800.9	3024.8	3788.6	2882.2	9303.4	3518.8	14400	0
c. 60 minute decay period								
	10%		25%		50%		75%	
	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
colony 1	2443.7	2172.4	3850.9	2380.7	5574.4	2310.2	13031.2	1365.9
colony 2	5259.6	4993.2	7700.3	4243.8	14364.8	64.88	14400	0
colony 3	2736.4	2843.8	3609.4	2728.7	6575.4	3356.4	13233.4	3135.5
d. 90 minute decay period								
	10%		25%		50%		75%	
	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
colony 1	2300.9	1516	3605.1	1732.8	5330	1958.6	9283	3170.3
colony 2	4395	3906.6	6711.5	3605.3	12409.6	2895	14400	0
colony 3	2562.8	2181.5	3456.3	2171.9	5594.4	2648.9	9503.9	3362.5

Table 6.6: Statistical results for minimum time to reach certain colony saturation percentages as a function of ant behavioral type.

Kruskal-Wallis χ^2 and p-values for differences in the minimum time for a seed ant to reach 10%, 25%, 50%, and 75% colony saturation when decay periods are (a) 15 minutes, (b) 30 minutes, (c) 60 minutes, and (d) 90 minutes. Asterisks represent statistically significant differences between groups at $\alpha = 0.05$ level. Degrees of freedom for all tests = 3.

Kruskal-Wallis results								
a. 15 minute decay period								
	10%		25%		50%		75%	
	χ^2	<i>p-value</i>	χ^2	<i>p-value</i>	χ^2	<i>p-value</i>	χ^2	<i>p-value</i>
colony 1	5.6089	0.132	7.623	0.054	-	-	-	-
colony 2	3.2961	0.348	-	-	-	-	-	-
colony 3	4.7069	0.1946	4.3605	0.2251	-	-	-	-
b. 30 minute decay period								
	10%		25%		50%		75%	
	χ^2	<i>p-value</i>	χ^2	<i>p-value</i>	χ^2	<i>p-value</i>	χ^2	<i>p-value</i>
colony 1	6.023	0.1105	7.2	0.0658	0.441	0.9316	-	-
colony 2	4.113	0.2495	0.98	0.805	-	-	-	-
colony 3	4.4912	0.2131	4.202	0.2405	1.776	0.6201	-	-
c. 60 minute decay period								
	10%		25%		50%		75%	
	χ^2	<i>p-value</i>	χ^2	<i>p-value</i>	χ^2	<i>p-value</i>	χ^2	<i>p-value</i>
colony 1	5.65	0.1298	7.7819	0.0507	5.1213	0.1631	1.0716	0.7839
colony 2	4.821	0.1854	4.6731	0.1974	5.294	0.1154	-	-
colony 3	4.4811	0.214	3.8279	0.2807	4.9586	0.1749	0.8918	0.8274
d. 90 minute decay period								
	10%		25%		50%		75%	
	χ^2	<i>p-value</i>	χ^2	<i>p-value</i>	χ^2	<i>p-value</i>	χ^2	<i>p-value</i>
colony 1	5.6516	0.1298	7.8756	0.048*	5.326	0.1494	1.31	0.7266
colony 2	5.1241	0.1629	4.83	0.1847	2.6705	0.4453	-	-
colony 3	4.5003	0.2123	3.8473	0.2784	3.3276	0.3438	2.8915	0.4087

Synthesis and general discussion

Ants are one of the most ecologically successful groups of organisms on Earth [5, 6] and are critical members of the ecological communities in which they reside [5, 13]. To understand their success, we need to understand how ants have contended with one of the presumed steepest costs of social living- the increased burden of infectious disease. Ant colonies exhibit many features, such as large population sizes [5, 88, 89] and higher than average genetic relatedness [5] that suggest that they would be particularly vulnerable to outbreaks of infectious disease. However, our knowledge of the parasitic organisms infecting ants has remained limited and we have little information on how these parasites impact ant colony functioning and survival. In this dissertation, I advance our knowledge by investigating three broad questions: (1) what are the life-history strategies and taxonomic patterns of parasitic organisms infecting ants, (2) what are the epidemiological impacts of these parasites on colony dynamics, and (3) how do ants mitigate the costs associated with parasitic organisms?

7.1 Major findings from this dissertation

What parasites infect ants?

In order to understand how ants have both managed their disease burden and been shaped by parasite selective pressure, we need to understand the life-histories of the parasitic organisms that infect them. In Chapter 2, I collected all known published records of parasitic organisms infecting ants and scored them for relevant life-history information, such as how they initially encounter their ant host, whether they cause

morbidity or mortality, whether they use direct or indirect life cycles, and whether they need to leave the nest before being capable of transmission to the next ant host.

Results from this extensive meta-analysis show that most parasitic organisms infecting ants require encountering their host in the extranidal (outside of the nest) environment. For many ant species, a robust division of labor coupled with stable nesting sites means that only a limited proportion of the colony likely becomes exposed to parasitic organisms in the first place. For individuals that do become infected, host death is likely because the majority of parasitic organisms infecting ants are parasitoids, which require the ant host's death as a developmental necessity.

Research in this field over the last three decades has focused almost exclusively on uncovering mechanisms by which ants could prevent disease transmission inside their nests. However, this work makes the fundamental assumption that parasites infecting ants are capable of intra-colony transmission. Thus, a major finding from this work is that the majority of parasitic organisms infecting ants use an '*ex-nido*' transmission strategy, and thus are incapable of direct, ant - to - ant transmission inside the nest.

In addition to uncovering general trends in parasite life history strategies, we were also interested in general taxonomic trends for both parasites and their ant hosts. From our extensive survey of published parasite records (1,415 records, 614 parasite species infecting 579 unique host species, Table A.1), we found that flies (Diptera) are the most prevalent group reported infecting ants, followed by fungi, and then parasitic wasps (Hymenoptera). Reports of viruses and bacteria infecting ants are surprisingly scarce. Methodological advances will allow for easier surveillance of viruses and bacteria infecting ants, and more records will undoubtedly follow as more sampling is conducted. However, even in the face of under sampling, there are many reports of bacteria associated with ants and their nest environs, but only one of these had any demonstrated pathogenicity to its host. The ecological and evolutionary reasons for the paucity of records of pathogenic bacteria and viruses infecting ants deserves more attention.

On the host side, only 10 out of 17 extant ant sub-families and 81 out of 333 extant ant genera have any parasite records associated with them. Many ant genera have been under sampled, due to ecologies that make them more difficult to study in the first place, and because they are not invasive or pestiferous and therefore not research priorities. Our knowledge of parasitic organisms infecting ants remains crippled by the lack of targeted research in this area, and we can expect many more records to be

added once we actually go out looking for them.

How do parasites impact colony dynamics?

In chapter 2, I found that most parasitic organisms infecting ants encounter their hosts in the extranidal environment, cause host death as developmental necessity, and require a period of time outside the nest before transmission to the next ant host can occur. In chapter 3, I investigated the impact of these parasitic organisms on ant colony dynamics using a deterministic model of mature ant colonies with and without the presence of the aforementioned parasites.

The model predicts that under biologically realistic parameter values, reductions in colony size may occur, but ant colonies are unlikely to suffer from parasite-induced collapse (Figure 3.4). Model predictions depend most heavily on the parasite force of infection term, which is a combination of how frequently foraging ants forage, how frequently foragers encounter parasites whilst out foraging, and the probability of parasite encounters resulting in successful infections. We lack empirical estimates for this term for most parasites infecting ants, and future work is needed if we are to understand how much pressure parasites exert on ant colonies. Our model predictions are also sensitive to the proportion of the colony in the forager compartment, but our empirical knowledge of what percentage of colonies forage and how ecological factors impact this proportion is also lacking. In sum, this chapter points to the conclusion that many parasites infecting ants are unlikely to result in colony collapse, and instead may cause negligible to moderate reductions in colony size. Understanding how colonies remain resilient to worker losses, and how these losses ultimately impact colony fitness, remain open questions.

While parasites that transmit outside of ant nests may dominate the records we found in Chapter 2, parasites that are capable of within-nest, ant-to-ant transmission are nevertheless important to understand. In Chapter 4, we explored the impacts of these parasites by using a stochastic compartmental modeling approach. We found that contrary to the parasite type modeled in Chapter 3, *in-nido* parasites are likely to result in catastrophic colony collapse and thus likely represent a strong selective force on ant colonies and potentially on the parasites themselves.

What can ant colonies do to mitigate disease pressure?

Ant colonies have a suite of anti-parasite defenses (reviewed in [91, 97, 99, 127, 129]) that are likely important in reducing the impact of infection by *in-nido* parasites. These include physiological, behavioral, and organizational defenses that can operate prophylactically or be induced in response to infection. In Chapter 4, I investigated how two behavioral defenses, behavioral avoidance and corpse management, could serve to mitigate impacts due to *in-nido* parasite infection. With corpse management, ants can reduce subsequent intra-colony transmission events by reducing the amount of time cadavers remain infectious, either by mechanically destroying cadavers or chemically inactivating them. With behavioral avoidance, ants can prevent infection and onward disease spread by recognizing infectious cadavers and limiting contact with them. In the stochastic modeling framework we employed, we showed that corpse management and behavioral avoidance of infectious cadavers could reduce colony collapse due to *in-nido* parasitism. Thus work from this chapter suggests that behavioral immune mechanisms can be important and effective means of controlling infection by the select few parasites that are capable of transmission inside ant colonies.

In Chapters 5 and 6, I investigated whether organizational immunity might be present in the social network and spatial structuring of colonies of the black carpenter ant, *Camponotus pennsylvanicus*. I focused on trophallaxis as the key social interaction because ant colonies must balance the efficient distribution of beneficial resources (i.e. food) while minimizing the transmission of the few parasites that are capable of per os transmission. In Chapter 5, I found evidence for the social and spatial segregation of forager ants from the queen. Foragers engaged in more trophallaxis events than other ants, but never directly interacted with the queen. Additionally, they spent more time in chambers closer to the nest entrance, away from the queen. In Chapter 6, I extended this investigation by looking for evidence of nuanced organizational immunity in the temporal structuring of carpenter ant trophallaxis networks. I found that foragers and queens are indeed socially segregated; they never directly interact with each other, although the mechanism underlying this social segregation remains unclear. However, we did not find evidence of nuanced protection against disease transmission in the temporal structuring of the trophallaxis networks; food originating from foragers did not take longer or have to go through more intermediaries to reach

the queen. Furthermore, theoretical spread analyses indicate that the diffusive reach of food originating from foragers is not different from that of other ant behavioral types. Other empirical work suggests that ant and other social insect colonies are optimized for fast food distribution [477, 498, 504], and the direct segregation of foragers and queens may provide sufficient enough protection against per os transmitting parasites.

7.2 Open questions and future work

This dissertation has contributed to a greater understanding of the ecology, epidemiology, and evolutionary impacts of parasites infecting ants. It has helped illuminate some gaps in our knowledge and areas where future research is much needed, discussed briefly below.

What parasite pressure do ant colonies naturally face?

In Chapter 2, I collected as many records of parasites infecting ants as I could in order to illuminate patterns in their ecology. However, the total diversity of parasites infecting ants is not what a single colony faces on a daily basis. What types of parasites do colonies interact with most frequently? How intensely do these parasites exert pressure on colonies and how much does this vary seasonally, with latitude, or other ecological or biogeographic factors?

To what extent does ant ecology predict parasite association?

Among the 13,000+ ant species, there are a wide range of nesting and foraging ecologies, from subterranean ants to arboreal nesting species, and from skilled predators to fungivorous farmers. In addition, there is a huge range in ant colony sizes (from tens to millions, reviewed in [88, 89]) and colony founding strategies. Do these host ecological traits predispose ant species or genera to parasitism by certain types of parasites? I hope to explore this in future work by using machine learning techniques (e.g. boosted regression trees) and a database of host ecological traits to see whether certain parasites are associated with ant species that have particular nesting or foraging ecologies.

How does ant and parasite evolutionary history predict parasite association?

The pattern of association between ants and their parasites is a result of both their ecological traits and their evolutionary pasts. The well-resolved phylogeny of the ants [4, 30] means that we are well poised to begin answering this question. In future work, I hope to look for signatures of co-evolutionary dynamics between ants and their parasites.

How does worker loss affect colony fitness?

A key finding of my dissertation is that the majority of parasites infecting ants use an *ex-nido* transmission strategy, which precludes intra-colony transmission and likely does not cause colony collapse. However, these parasites still do remove individuals from colonies, and we lack understanding of exactly how colonies buffer these losses and what the ultimate, colony-level, consequences of these losses are. What are the impacts of losing 10% of the colony vs. 50% of the colony? How does losing a certain behavioral caste impact colony functioning and fitness? A related question to this is whether ant social or spatial networks change in the presence of parasitism, and how this impacts emergent, colony-level behaviors. Understanding how colonies remain resilient to parasite-induced perturbations or loss is key to understanding their larger ecological success.

Taken together, the work of my dissertation has furthered our understanding of large-scale patterns in the ecology of parasites infecting ants, explored how these parasites interact epidemiologically with their ant hosts and has investigated potential mechanisms that ants might have evolved to combat infection pressure by their parasites.

APPENDIX A

A

Supplementary Information for Chapter 2

Here I present an abridged version of the database of records of parasites and parasitoids infecting ants in table A.1. A full version of this database, including records for non-parasitic associates, will be made available upon publication of this work.

A.1 Ant parasite database

Table A.1: Database of parasites and parasitoids infecting ants

Ant parasite database							
Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Virus	Dicistroviridae	<i>Aparavirus: Kashmir bee virus</i>	<i>Linepithema humile</i>	A	1	Dir.	In
Virus	Dicistroviridae	<i>Aparavirus: Solenopsis invicta virus-1</i>	<i>Solenopsis invicta</i>	A	1	Dir.	In
Virus	Dicistroviridae	<i>Aparavirus: Solenopsis invicta virus-1</i>	<i>Solenopsis carolinensis</i>	A	1	Dir.	In
Virus	Dicistroviridae	<i>Aparavirus: Solenopsis invicta virus-1</i>	<i>Solenopsis geminata</i>	A	1	Dir.	In
Virus	Dicistroviridae	<i>Aparavirus: Solenopsis invicta virus-1</i>	<i>Solenopsis richteri</i>	A	1	Dir.	In
Virus	Dicistroviridae	<i>Linepithema humile virus-1</i>	<i>Linepithema humile</i>	A	1	Dir.	In
Virus	Dicistroviridae	<i>Triatovirus: Black queen cell virus</i>	<i>Linepithema humile</i>	A	1	Dir.	In
Virus	Iflaviridae	<i>Iflavirus: Deformed wing virus</i>	<i>Linepithema humile</i>	A	1	Dir.	In
Virus	IncertaeSedis	<i>Chronic bee paralysis virus</i>	<i>Camponotus vagus</i>	A	1	Dir.	In
Virus	IncertaeSedis	<i>Chronic bee paralysis virus</i>	<i>Formica rufa</i>	A	1	Dir.	In
Virus	Parvoviridae	<i>Hymenopteran ambidensovirus 1</i>	<i>Solenopsis invicta</i>	A	1	Dir.	In
Virus	Picornaviridae?	<i>Solenopsis invicta virus-2</i>	<i>Solenopsis invicta</i>	A	1	Dir.	In
Virus	Picornaviridae?	<i>Solenopsis invicta virus-2</i>	<i>Solenopsis invicta x richteri</i>	A	1	Dir.	In

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Virus	Soliniviridae	<i>Invictavirus: Solenopsis invicta virus-3</i>	<i>Solenopsis invicta</i>	A	1	Dir.	In
Virus	Soliniviridae	<i>Invictavirus: Solenopsis invicta virus-3</i>	<i>Solenopsis geminata x xyloni</i>	A	1	Dir.	In
Bacteria	Pseudomonadaceae	<i>Pseudomonas sp.</i>	<i>Solenopsis sp.</i>	A	1	Dir.	In
Fungi	Ancylistaceae	<i>Conidiobolus macrosporus</i>	<i>Solenopsis invicta</i>	B	1	Dir.	In
Fungi	Clavicipitaceae	<i>Metarhizium anisopliae</i>	<i>Atta sexdens rubropilosa</i>	B	1	Dir.	In
Fungi	Clavicipitaceae	<i>Metarhizium anisopliae</i>	<i>Paratrechina longicornis</i>	B	1	Dir.	In
Fungi	Clavicipitaceae	<i>Metarhizium anisopliae</i>	<i>Solenopsis invicta</i>	B	1	Dir.	In
Fungi	Clavicipitaceae	<i>Metarhizium anisopliae</i>	<i>Leptogenys sp.</i>	B	1	Dir.	In
Fungi	Clavicipitaceae	<i>Metarhizium anisopliae</i>	<i>Solenopsis invicta</i>	B	1	Dir.	In
Fungi	Clavicipitaceae	<i>Metarhizium anisopliae</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	In
Fungi	Clavicipitaceae	<i>Metarhizium brunneum</i>	<i>Formica selysi</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Pachycondyla tarsata</i>	B	1	Dir.	Ex
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Paltothyreus tarsatus</i>	B	1	Dir.	Ex
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Camponotus brutus</i>	B	1	Dir.	Ex
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Crematogaster bequaerti</i>	B	1	Dir.	Ex
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Crematogaster clariventris</i>	B	1	Dir.	Ex
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Crematogaster striatula</i>	B	1	Dir.	Ex
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Dorylus sp.</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species				
				Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Macromischoides aculeatus</i>	B	1	Dir.	Ex
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Macromischoides inermis</i>	B	1	Dir.	Ex
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Oecophylla longinoda</i>	B	1	Dir.	Ex
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Platythyrea conradti</i>	B	1	Dir.	Ex
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Polyrhachis decemdentata</i>	B	1	Dir.	Ex
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Polyrhachis militaris</i>	B	1	Dir.	Ex
Fungi	Cordycipitaceae	<i>Akanthomyces gracilis</i>	<i>Polyrhachis monista</i>	B	1	Dir.	Ex
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Acromyrmex lundii</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Atta lundii</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Formica sp.</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Atta sp.</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Solenopsis richteri</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Cephalotes atratus</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Ectatomma ruidum</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Paraponera clavata</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Crematogaster sp.</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Atta mexicana</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Formica selysi</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Myrmecia nigricapax</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Solenopsis invicta</i>	B	1	Dir.	In

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species				
				Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Oecophylla smarginada</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Lasius fuliginosus</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Atta texana</i>	B	1	Dir.	In
Fungi	Cordycipitaceae	<i>Beauveria bassiana</i>	<i>Camponotus sp.</i>	B	1	Dir.	In
Fungi	Entomophthoraceae	<i>Pandora formicae</i>	<i>Formica polyctena</i>	B	1	Dir.	Ex
Fungi	Entomophthoraceae	<i>Pandora formicae</i>	<i>Formica exsecta</i>	B	1	Dir.	Ex
Fungi	Entomophthoraceae	<i>Pandora formicae</i>	<i>Formica pratensis</i>	B	1	Dir.	Ex
Fungi	Entomophthoraceae	<i>Pandora formicae</i>	<i>Formica polyctena</i>	B	1	Dir.	Ex
Fungi	Entomophthoraceae	<i>Pandora formicae</i>	<i>Formica rufa</i>	B	1	Dir.	Ex
Fungi	Entomophthoraceae	<i>Pandora formicae</i>	<i>Lasius sp.</i>	B	1	Dir.	Ex
Fungi	Entomophthoraceae	<i>Pandora formicae</i>	<i>Formica cf. lemani</i>	B	1	Dir.	Ex
Fungi	Entomophthoraceae	<i>Pandora myrmecophaga</i>	<i>Formica exsecta</i>	B	1	Dir.	Ex
Fungi	Entomophthoraceae	<i>Pandora myrmecophaga</i>	<i>Formica polytecnica</i>	B	1	Dir.	Ex
Fungi	Entomophthoraceae	<i>Pandora myrmecophaga</i>	<i>Formica pratensis</i>	B	1	Dir.	Ex
Fungi	Entomophthoraceae	<i>Pandora myrmecophaga</i>	<i>Formica rufa</i>	B	1	Dir.	Ex
Fungi	Entomophthoraceae	<i>Pandora myrmecophaga</i>	<i>Formica lemani</i>	B	1	Dir.	Ex
Fungi	Entomophthoraceae	<i>Tarichium sp.</i>	<i>Tetramorium caespitum</i>	B	1	Dir.	Ex
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella maroccana</i>	<i>Aphaenogaster baronii</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella roussillonensis</i>	<i>Cataglyphis cursor</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella sp.</i>	<i>Polyergus breviceps</i>	A	1	Dir.	Unknown

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella superficialis</i>	<i>Formica exsecta</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella superficialis</i>	<i>Formica sanguinensis</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella superficialis</i>	<i>Formica polyctena</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella superficialis</i>	<i>Formica lugubris</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella superficialis</i>	<i>Formica pratensis</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella superficialis</i>	<i>Formica truncorum</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella superficialis</i>	<i>Formica rufa</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella superficialis</i>	<i>Formica fusca</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella superficialis</i>	<i>Formica sanguinea</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella superficialis</i>	<i>Formica decipiens</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella tuberculata</i>	<i>Lasius grandis</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella tuberculata</i>	<i>Lasius nitidigaster</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella tuberculata</i>	<i>Lasius distinguendus</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella tuberculata</i>	<i>Lasius umbratus</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella tuberculata</i>	<i>Formica fusca</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella tuberculata</i>	<i>Lasius flavus</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella tuberculata</i>	<i>Formica pressilabris</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella tuberculata</i>	<i>Formica rufa</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella tuberculata</i>	<i>Formica rufibarbis</i>	A	1	Dir.	Unknown
Fungi	<i>Incertae Sedis</i>	<i>Aegeritella tuberculata</i>	<i>Lasius pallitarsis</i>	A	1	Dir.	Unknown

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	<i>Incertae Sedis</i>	<i>Hormiscium myrmecophilum</i>	<i>Pseudomyrmex sp.</i>	A	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Hormiscium myrmecophilum</i>	<i>Myrmica sp.</i>	A	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Hormiscium myrmecophilum</i>	<i>Myrmica sabuleti</i>	A	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Plagiolepis vInd.obonensis</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Tetramorium sp. D</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Solenopsis fugax</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Tetramorium sp. E</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Temnothorax affinis</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Temnothorax recedens</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Temnothorax unifasciatus</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Plagiolepis pygmaea</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Pheidole williamsi</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Cardiocondyla elegans</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Pheidole pallidula</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Temnothorax tuberum</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Plagiolepis taurica</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Tetramorium casepitem</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Temnothorax albipennis</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Temnothorax angustulus</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Temnothorax exilis</i>	B	1	Dir.	In

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Temnothorax muellerianus</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Temnothorax nylanderi</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Temnothorax racovitzai</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Aphaenogaster senilis</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Cataglyphis hispanica</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Crematogaster auberti</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Gonionomma hispanicum</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Messor barbarus</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Tapinoma nigerrimum</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Tapinoma simrothi</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Strongylognathus caeciliae</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Temnothorax lichtensteini</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Tetramorium semilaeve</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Solenopsis sp.</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Pogonomyrmex barbatus</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Pheidole bicarinata</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Pogonomyrmex badius</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Solenopsis carolinensis</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Strumigenys membranifera</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Nylanderia vividula</i>	B	1	Dir.	In

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Pheidole tysoni</i>	B	1	Dir.	In
Fungi	<i>Incertae Sedis</i>	<i>Myrmicinosporidium durum</i>	<i>Solenopsis invicta</i>	B	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia camponoti</i>	<i>Camponotus universitatis</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia camponoti</i>	<i>Camponotus sp.</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia camponoti</i>	<i>Camponotus aethiops</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia camponoti</i>	<i>Camponotus pilicornis</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia camponoti</i>	<i>Camponotus sylvaticus</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia camponoti</i>	<i>Camponotus baldacci</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Lasius alienus</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Lasius neglectus</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Lasius niger</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Lasius grandis</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Formica argentea</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Formica aserva</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Formica curiosa</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Formica incerta</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Formica lasioides</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Formica montana</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Formica neogagates</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Formica pallidefulva</i>	A	1	Dir.	In

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species				
				Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Formica puberula</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Formica subintegra</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Formica subpolita</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Formica subsericea</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Formica vinculans</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Lasius alienus</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Lasius murphyi</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Lasius neoniger</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Lasius pallitarsis</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Myrmecocystus mimicus</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Polyergus breviceps</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Polyergus lucidus</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Laboulbenia formicarium</i>	<i>Prenolepis imparis</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Rickia sp. 1</i>	<i>Messor sp.</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Rickia wasmanni</i>	<i>Myrmica rubra</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Rickia wasmanni</i>	<i>Myrmica scabrinodis</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Rickia wasmanni</i>	<i>Myrmica slovaca</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Rickia wasmanni</i>	<i>Myrmica rubra</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Rickia wasmanni</i>	<i>Myrmica vandeli</i>	A	1	Dir.	In
Fungi	Laboulbeniaceae	<i>Rickia wasmanni</i>	<i>Myrmica specioides</i>	A	1	Dir.	In

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Laboulbeniaceae	<i>Rickia wasmanni</i>	<i>Myrmica sabuleti</i>	A	1	Dir.	In
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps acerosa</i>	<i>Camponotus sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps albacongiuae</i>	<i>Camponotus sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Camponotus hapax</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Cephalotes atratus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Pachycondyla crenada</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Pachycondyla curvinodis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Pachycondyla foetida</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Pachycondyla impressa</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Pachycondyla sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Pachycondyla striata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Pachycondyla villosa</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Pseudomyrmex termitarium</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Trachymyrmex cornetzi</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Odontomachus hastatus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Pachycondyla crassinoda</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Paraponera clavata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Pachycondyla apicalis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Pachycondyla striata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Pachycondyla pachyderma</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species				
				Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Pachycondyla tarsata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Paltothyreus tarsatus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Bothroponera</i> sp.	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Dinoponera</i> sp.	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps australis</i>	<i>Phrynoponera</i> sp.	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps blakebarnesii</i>	<i>Camponotus</i> sp.	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps atricipis</i>	camponoti- <i>Camponotus atriceps</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps balzani</i>	camponoti- <i>Camponotus balzani</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps bispinosi</i>	camponoti- <i>Camponotus bispinosus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps chartificis</i>	camponoti- <i>Camponotus chartifex</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps femorati</i>	camponoti- <i>Camponotus femoratus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps floridani</i>	camponoti- <i>Camponotus floridanus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps hippocrepidis</i>	camponoti- <i>Camponotus hippocrepis</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species		Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps Ind.iani</i>	<i>camponoti-</i>	<i>Camponotus Ind.ianus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps leonardi</i>	<i>camponoti-</i>	<i>Camponotus leonardi</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps melanotici</i>	<i>camponoti-</i>	<i>Camponotus melanoticus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps nidulantis</i>	<i>camponoti-</i>	<i>Camponotus niduland</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps novogranadensis</i>	<i>camponoti-</i>	<i>Camponotus novogranadensis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps renggeri</i>	<i>camponoti-</i>	<i>Camponotus renggeri</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps rufipedis</i>	<i>camponoti-</i>	<i>Camponotus rufipes</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps saundersi</i>	<i>camponoti-</i>	<i>Camponotus saundersi</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps sexguttati</i>	<i>camponoti-</i>	<i>Camponotus sexguttatus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps daceti</i>		<i>Daceton armigerum</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>		<i>Camponotus auriventris</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Camponotus dolichoderoides</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Camponotus gigas</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Camponotus leonardi</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Camponotus praeruta</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Camponotus rufifemer</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Camponotus saundersi</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Echinopla lineata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Polyrhachis armata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Polyrhachis bicolor</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Polyrhachis calypso</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Polyrhachis furcata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Polyrhachis halidayi</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Polyrhachis hauxwelli</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Polyrhachis hippomanes</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Polyrhachis illaudata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Polyrhachis proxima</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps formicarum</i>	<i>Polyrhachis rastellata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps halabalaensis</i>	<i>Camponotus gigas</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Camponotus auriventris</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Camponotus singularis</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Diacamma rugosum</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Polyrhachis abdominalis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Polyrhachis armata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Polyrhachis bicolor</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Polyrhachis bihamata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Polyrhachis furcata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Polyrhachis halidayi</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Polyrhachis hippomanes</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Polyrhachis illaudata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Polyrhachis proxima</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Polyrhachis spp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps irangiensis</i>	<i>Tetraponera attenuata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kimflemingiae</i>	<i>Camponotus castaneus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Cephalotes sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Dolichoderus attelaboides</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Dolichoderus sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Dolichoderus sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Gnamptogenys sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Gnamptogenys sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Pachycondyla moesta</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Pachycondyla sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Pachycondyla villosa</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Paraponera clavata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Cephalotes atratus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Dolichoderus spinosa</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Myrmica rubra</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps kniphofioides</i>	<i>Acromyrmex octospinosus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps lloydii binata</i>	<i>Camponotus sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps lloydii lloydii</i>	<i>Camponotus abdominalis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps lloydii s.l.</i>	<i>Dolichoderus thoracicus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps monacidis</i>	<i>Dolichoderus bispinosus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmecophila</i>	<i>Polyrhachis robsoni</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmecophila</i>	<i>Polyrhachis armata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmecophila</i>	<i>Camponotus auriventris</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmecophila</i>	<i>Camponotus singularis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmecophila</i>	<i>Diacamma rugosum</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmecophila</i>	<i>Polyrhachis abdominalis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmecophila</i>	<i>Polyrhachis bicolor</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmecophila</i>	<i>Polyrhachis bihamata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmecophila</i>	<i>Polyrhachis furcata</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmecophila</i>	<i>Polyrhachis halidayi</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmecophila</i>	<i>Polyrhachis illaudata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmecophila</i>	<i>Polyrhachis proxima</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmecophila</i>	<i>Polyrhachis spp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmicarum</i>	<i>Myrmica rubra</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmicarum</i>	<i>Crematogaster bequaerti</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmicarum</i>	<i>Crematogaster cf. gabonensis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmicarum</i>	<i>Crematogaster clariventris</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmicarum</i>	<i>Crematogaster striatula</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmicarum</i>	<i>Macromischoides inermis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps myrmicarum</i>	<i>Tetramorium aculeatus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps naomipierceae</i>	<i>Polyrhachis cf. robsonii</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps oecophyllae</i>	<i>Oecophylla smaragdina</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps ootaki</i>	<i>Polyrhachis sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps ovalispora</i> var. <i>dolichoderi</i>	<i>Dolichoderus attelaboides</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps ovalispora</i> var. <i>ovalispora</i>	<i>Cephalotes atratus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps polyrhachis-furcata</i>	<i>Polyrhachis furcata</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps ponerinarum</i>	<i>Paraponera clavata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps pseudolloydii</i>	<i>Polyrhachis robsoni</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps rami</i>	<i>Camponotus sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps satoi</i>	<i>Polyrhachis sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps septa</i>	<i>Camponotus sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps sp.</i>	<i>Crematogaster sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps sp.</i>	<i>Pachycondyla tarsata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps sp. (GH 41)</i>	<i>Polyrhachis sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps subramanianii</i>	<i>Pachycondyla sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps subramanianii</i>	<i>Myrmica rubra</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps subramanianii</i>	<i>Atta colombica</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus apicalis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus cf. femoratus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus cf. helleri</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus chantifex</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus crassus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus nidulans</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus prox. Sexguttatus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus rectangularis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus senex</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus sexguttatus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus sericeiventris</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus abdominalis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus brutus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus vividus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Oecophylla longinoda</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Phasmomyrmex aberrans</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Phasmomyrmex buchneri</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Phasmomyrmex decemdentata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Phasmomyrmex paradoxa</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis decemdentata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis fissa</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis laboriosa</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis latharis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis latispina</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis militaris</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis monista</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis revoili</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis sulcata</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Echinopla melanarctos</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis rufofemorata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis lamellidens</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus gigas</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis illaudata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus dolichoderoides</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus leonardi</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus praeruta</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus rufifemer</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Echinopla sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis armata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis bicolor</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis furcata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis halidayi</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis hauxwelli</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis hippomanes</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis proxima</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Polyrhachis rastellata</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus americanus</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus castaneus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus ligniperdus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Ophiocordyceps unilateralis</i>	<i>Camponotus pennsylvanicus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Polycephalomyces cyllInd.rosporus</i>	<i>Dorylus sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Polycephalomyces cyllInd.rosporus</i>	<i>Paltothyreus tarsatus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Stilbella buquetti var. formicarum</i>	<i>Dolichoderus attelaboides</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Stilbella buquetti var. formicarum</i>	<i>Crematogaster bequaerti</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Stilbella buquetti var. formicarum</i>	<i>Crematogaster clariventris</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Stilbella buquetti var. formicarum</i>	<i>Crematogaster striatula</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Stilbella buquetti var. formicarum</i>	<i>Macromischoides inermis</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Stilbella buquetti var. formicarum</i>	<i>Paltothyreus tarsatus</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Stilbella burmensis</i>	<i>Oecophylla longinoda</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Stilbella burmensis</i>	<i>Camponotus sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Stilbella dolichoderinarum</i>	<i>Technomyrmex sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Stilbella sp.</i>	<i>Crematogaster sp.</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Stilbella spp.</i>	<i>Oecophylla smaragdina</i>	B	1	Dir.	Ex
Fungi	Ophiocordycipitaceae	<i>Stilbum burmense</i>	<i>Oecophylla longinoda</i>	B	1	Dir.	Ex
Fungi	Pleosporaceae	<i>Alternaria tenuis</i>	<i>Formica rufa</i>	B	1	Dir.	Ex
Fungi	Trichocomaceae	<i>Aspergillus flavus</i>	<i>Atta sp.</i>	B	1	Dir.	In
Fungi	Trichocomaceae	<i>Aspergillus flavus</i>	<i>Acromyrmex echinatior</i>	B	1	Dir.	In

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species				
				Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Fungi	Trichocomaceae	<i>Aspergillus flavus</i>	<i>Atta texana</i>	B	1	Dir.	In
Fungi	Trichocomaceae	<i>Aspergillus flavus</i>	<i>Formica selysi</i>	B	1	Dir.	In
Fungi	Trichocomaceae	<i>Aspergillus flavus</i>	<i>Paratrechina longicornis</i>	B	1	Dir.	In
Fungi	Trichocomaceae	<i>Aspergillus flavus</i>	<i>Polyrhachis sp.</i>	B	1	Dir.	In
Fungi	Trichocomaceae	<i>Aspergillus flavus</i>	<i>Solenopsis richteri</i>	B	1	Dir.	In
Fungi	Trichocomaceae	<i>Aspergillus flavus</i>	<i>Solenopsis invicta</i>	B	1	Dir.	In
Microsporidia	Burenellidae	<i>Burenella dimorpha</i>	<i>Solenopsis geminata</i>	B	2	Dir.	In
Microsporidia	Burenellidae	<i>Burenella dimorpha</i>	<i>Solenopsis richteri</i>	B	2	Dir.	In
Microsporidia	Burenellidae	<i>Burenella dimorpha</i>	<i>Solenopsis sp.</i>	B	2	Dir.	In
Microsporidia	Burenellidae	<i>Vairimorpha invictae</i>	<i>Solenopsis invicta</i>	A	Mult.	Dir.	In
Microsporidia	Burenellidae	<i>Vairimorpha invictae</i>	<i>Solenopsis macdonaghi</i>	A	Mult.	Dir.	In
Microsporidia	<i>Incertae Sedis</i>	<i>Kneallhazia solenopsae</i>	<i>Solenopsis macdonaghi</i>	A	Mult.	Dir.	In
Microsporidia	<i>Incertae Sedis</i>	<i>Kneallhazia solenopsae</i>	<i>Solenopsis richteri</i>	A	Mult.	Dir.	In
Microsporidia	<i>Incertae Sedis</i>	<i>Kneallhazia solenopsae</i>	<i>Solenopsis sp.</i>	A	Mult.	Dir.	In
Microsporidia	<i>Incertae Sedis</i>	<i>Kneallhazia solenopsae</i>	<i>Solenopsis invicta</i>	A	Mult.	Dir.	In
Apicomplexa	Lipotrophidae	<i>Mattesia geminata</i>	<i>Solenopsis invicta</i>	B	2	Dir.	In
Apicomplexa	Lipotrophidae	<i>Mattesia geminata</i>	<i>Solenopsis geminata</i>	B	2	Dir.	In
Apicomplexa	Lipotrophidae	<i>Mattesia geminata</i>	<i>Leptothorax sp.</i>	B	2	Dir.	In
Apicomplexa	Lipotrophidae	<i>Mattesia nov. sp.</i>	<i>Solenopsis invicta</i>	B	2	Dir.	In
Trematoda	Dicrocoeliidae	<i>Brachylecithum mosquensis</i>	<i>Camponotus herculeanus</i>	B	1	Indir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species				
				Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Trematoda	Dicrocoeliidae	<i>Brachylecithum mosquensis</i>	<i>Camponotus pennsylvanicus</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium chinensis</i>	<i>Formica gagates</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Formica nigricans</i>	B	2	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Formica lugubris</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Formica polyctena</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Formica pratensis</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Formica fusca</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Formica cunicularia</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Formica gagates</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Formica rufa</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Formica rufibarbis</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Cataglyphis bicolor</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Lasius sp.</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Cataglyphis aenescens</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Formica cinerea</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Formica mesasiatica</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Formica picea</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium dendriticum</i>	<i>Formica sanguinea</i>	B	1	Indir.	Ex
Trematoda	Dicrocoeliidae	<i>Dicrocoelium hospes</i>	<i>Camponotus compressiscapus</i>	B	1	Indir.	Ex
Trematoda	Heterophyidae	<i>Eurytrema pancreaticum</i>	<i>Technomyrmex detorquens</i>	B	1	Indir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Cestoda	Davaineidae	<i>Cotugnia digonopora</i>	<i>Monomorium destructor</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Cotugnia digonopora</i>	<i>Monomorium floricola</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Cotugnia digonopora</i>	<i>Monomorium gracillimum</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Cotugnia digonopora</i>	<i>Monomorium salomonis Ind.icum</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Cotugnia digonopora</i>	<i>Pheidole fossulata</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Cotugnia digonopora</i>	<i>Monomorium sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina australis</i>	<i>Pheidole sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina beveridgei</i>	<i>Pheidole sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina caucasica</i>	<i>Tetramorium caespitum</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina chiltoni</i>	<i>Pheidole sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina circumvalata</i>	<i>Pheidole pattidula</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina circumvalata</i>	<i>Tetramorium casepitem</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina circumvalata</i>	<i>Pheidole sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina dromaius</i>	<i>Pheidole sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Pheidole bergi</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Pheidole pattidula</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Tetramorium caespitum</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Tetramorium semilaeve</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Monomorium salmonis Ind.ictum</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Pheidole fossulata</i>	B	2	Indir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Pheidologeton sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Prenolepis sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Tetramorium rothneyi</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Tetramorium similum</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Tetramorium sp. 1</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Tetramorium sp. 2</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Tetramorium tortosum</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Tetramorium caespitum jacoti</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Pheidole sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina echinobothrida</i>	<i>Pheidole vinelandica</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina fedjuschini</i>	<i>Tetramorium caespitum</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina friedbergeri</i>	<i>Formica rufa</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina georgiensis</i>	<i>Pheidole vinlandica</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina kashiwarensis</i>	<i>Brachyponera chinensis</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina loeweni</i>	<i>Pheidole bicarinata</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina loeweni</i>	<i>Pheidole sitarches campestris</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina mehrai</i>	<i>Pheidole sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina mitchelli</i>	<i>Pheidole sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina singhi</i>	<i>Pheidole sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Monomorium floricola</i>	B	2	Indir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Monomorium salmonis Ind.icum</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Monomorium scabriceps</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Monomorium sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Pheidole fossulata</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Pheidole rhombinoda</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Tetramorium rothneyi</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Tetramorium simillium</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Tetramorium sp. 2</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Tetramorium tortosum</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Pheidole sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Pheidole fervida</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Tetramorium caespitum jacoti</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Tetramorium caespitum</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Pachycondyla sennaarensis</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Pheidole vinelandica</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Crematogaster lineolata</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Iridomyrmex pruinosus</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Pheidole dentata</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Prenolepis sp.</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina tetragona</i>	<i>Solenopsis molesta</i>	B	2	Indir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Cestoda	Davaineidae	<i>Raillietina urogalli</i>	<i>Myrmica rubra</i>	B	2	Indir.	Ex
Cestoda	Davaineidae	<i>Raillietina urogalli</i>	<i>Myrmica scabrinodis</i>	B	2	Indir.	Ex
Cestoda	Dilepididae	<i>Anomotaenia brevis</i>	<i>Leptothorax nylanderi</i>	B	2	Indir.	Ex
Cestoda	Dilepididae	<i>Choanotaenia crateriformis</i>	<i>Leptothorax sp.</i>	B	2	Indir.	Ex
Cestoda	Mesocestoididae	<i>Mesocestoides sp.</i>	<i>Lasius niger</i>	B	2	Indir.	Ex
Cestoda	Mesocestoididae	<i>Mesocestoides sp.</i>	<i>Tapinoma sessile</i>	B	2	Indir.	Ex
Nematoda	Allantonematidae	<i>Formicitylenchus oregonensis</i>	<i>Camponotus vicinus</i>	A	2	Dir.	Ex
Nematoda	Allantonematidae	<i>Paleoallantonema cephalotae</i>	<i>Cephalotes serratus</i>	B	Unk.	Indir.	Ex
Nematoda	Diplogastridae	<i>Formicodiplogaster myrmenema</i>	<i>Azteca alpha</i>	A	Mult.	Indir.	Ex
Nematoda	Diplogastridae	<i>Pristonchus sp.</i>	<i>Atta cephalotes</i>	A	Mult.	Indir.	Ex
Nematoda	Heterorhabditae	<i>Heterorhabditis bacteriophora</i>	<i>Solenopsis invicta</i>	B	Mult.	Indir.	Ex
Nematoda	Heterorhabditae	<i>Heterorhabditis bacteriophora</i>	<i>Solenopsis richteri</i>	B	Mult.	Indir.	Ex
Nematoda	Mermithidae	<i>Agamomermis cephaloti</i>	<i>Cephalotes minutus</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Agamomermis costaricensis</i>	<i>Odontomachus hastatus</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Agamomermis ecitoni</i>	<i>Eciton burchellii</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Allomermis solenopsi</i>	<i>Solenopsis invicta</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Camponotimermis bifidus</i>	<i>Camponotus aethiops</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Comanimermis clujensis</i>	<i>Camponotus aethiops</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Comanimermis clujensis</i>	<i>Formica fusca</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Heydenius formicinus</i>	<i>Prenolepis henschei</i>	B	Unk.	Indir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species				
				Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Nematoda	Mermithidae	<i>Heydenius myrmecophila</i>	<i>Linepithema sp.</i>	B	Unk.	Indir.	Ex
Nematoda	Mermithidae	<i>Mermis sp.</i>	<i>Ectatomma tuberculatum</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Meximermis ectatommi</i>	<i>Ectatomma ruidum</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Pheromermis lasiusi</i>	<i>Lasius niger</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Pheromermis myrmecophila</i>	<i>Lasius flavus</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Pheromermis myrmecophila</i>	<i>Lasius niger</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Pheromermis myrmecophila</i>	<i>Lasius sp.</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Pheromermis villosa</i>	<i>Lasius flavus</i>	B	2	Indir.	Ex
Nematoda	Mermithidae	<i>Pheromermis villosa</i>	<i>Lasius niger</i>	B	2	Indir.	Ex
Nematoda	Panagrolaimidae	<i>Panagrolaimus sp.</i>	<i>Atta cephalotes</i>	A	Mult.	Indir.	Ex
Nematoda	Panagrolaimidae	<i>Panagrolaimus sp.</i>	<i>Acromyrmex crassispinus</i>	A	Mult.	Indir.	Ex
Nematoda	Physalopteridae	<i>Skrjabinoptera phrynosoma</i>	<i>Pogonomyrmex barbatus</i>	A	2	Indir.	Ex
Nematoda	Rhabditidae	<i>Diplogasteroides spengelli</i>	<i>Lasius brunneus</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Diploscapter formicidae</i>	<i>Prolasius advenus</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Diploscapter lycostoma</i>	<i>Formica sp.</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Diploscapter lycostoma</i>	<i>Lasius sp.</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Diploscapter lycostoma</i>	<i>Myrmica rugulosa</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Diploscapter lycostoma</i>	<i>Azteca sp.</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Diploscapter lycostoma</i>	<i>Iridomyrmex humilis</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Diploscapter lycostoma</i>	<i>Linepithema humile</i>	A	Mult.	Indir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species				
				Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Nematoda	Rhabditidae	<i>Diploscapter sp.</i>	<i>Cladomyrma sp.</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Diploscapter sp.</i>	<i>Crematogaster sp.</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Diploscapter sp.</i>	<i>Lasius brunneus</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Diploscapter sp.</i>	<i>Solenopsis invicta</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Halicephalobus similigaster</i>	<i>Lasius brunneus</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Koerneria histophora</i>	<i>Lasius brunneus</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Mesorhabditis longespiculosa</i>	<i>Solenopsis invicta</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Oscheius dolichura</i>	<i>Camponotus herculeanus</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Oscheius dolichura</i>	<i>Lasius claviger</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Oscheius dolichura</i>	<i>Formica rufa</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Oscheius dolichura</i>	<i>Lasius brunneus</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Oscheius dolichura</i>	<i>Lasius flavus</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Oscheius dolichura</i>	<i>Lasius niger</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Oscheius dolichura</i>	<i>Tetramorium caespitum</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Oscheius dolichura</i>	<i>Formica polyctena</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Oscheius dolichura</i>	<i>Solenopsis invicta</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Pristionchus lheritieri</i>	<i>Formica rufa</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Pristionchus lheritieri</i>	<i>Lasius sp.</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Rhabditis janeti</i>	<i>Capritermes</i>	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Sclerorhabditis sp.</i>	<i>Cladomyrma sp.</i>	A	Mult.	Indir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Nematoda	Rhabditidae	<i>Sclerorhabditis</i> sp.	<i>Crematogaster</i> sp.	A	Mult.	Indir.	Ex
Nematoda	Rhabditidae	<i>Sclerorhabditis</i> sp.	<i>Solenopsis invicta</i>	A	Mult.	Indir.	Ex
Nematoda	Seuratidae	<i>Rabbiium paradoxus</i>	<i>Camponotus castaneus</i>	B	Mult.	Indir.	Ex
Nematoda	Steinernematidae	<i>Steinerema carpocapsae</i>	<i>Acromyrmex octospinosus</i>	B	Mult.	Indir.	Ex
Nematoda	Steinernematidae	<i>Steinerema carpocapsae</i>	<i>Camponotus</i> sp.	B	Mult.	Indir.	Ex
Nematoda	Steinernematidae	<i>Steinerema carpocapsae</i>	<i>Myrmica</i> sp.	B	Mult.	Indir.	Ex
Nematoda	Steinernematidae	<i>Steinerema carpocapsae</i>	<i>Pogonomyrmex</i> sp.	B	Mult.	Indir.	Ex
Nematoda	Steinernematidae	<i>Steinerema carpocapsae</i>	<i>Solenopsis geminata</i>	B	Mult.	Indir.	Ex
Nematoda	Steinernematidae	<i>Steinerema carpocapsae</i>	<i>Solenopsis invicta</i>	B	Mult.	Indir.	Ex
Nematoda	Steinernematidae	<i>Steinerema carpocapsae</i>	<i>Solenopsis richteri</i>	B	Mult.	Indir.	Ex
Nematoda	Steinernematidae	<i>Steinerema carpocapsae</i>	<i>Solenopsis</i> sp.	B	Mult.	Indir.	Ex
Nematoda	Tetradonematidae	<i>Myrmeconema antiqua</i>	<i>Cephalotes erratus</i>	B	Unk.	Indir.	Ex
Nematoda	Tetradonematidae	<i>Myrmeconema neotropicum</i>	<i>Cephalotes atratus</i>	B	2	Indir.	Ex
Nematoda	Tetradonematidae	<i>Tetradonema solenopsis</i>	<i>Solenopsis invicta</i>	B	Unk.	Indir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma berlinense</i>	<i>Camponotus vagus</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma berlinense</i>	<i>Camponotus</i> spp.	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma berlinense</i>	<i>Formica fusca</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma berlinense</i>	<i>Formica japonica</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma berlinense</i>	<i>Formica pratensis</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma berlinense</i>	<i>Formica rufa</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Braconidae	<i>Elasmosoma berlinense</i>	<i>Formica sanguinea</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma berlinense</i>	<i>Formica spp.</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma berlinense</i>	<i>Lasius niger</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma berlinense</i>	<i>Polyergus sp.</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma berlinense</i>	<i>Formica aquilonia</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma luxemburgense</i>	<i>Formica rufibarbis</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma luxemburgense</i>	<i>Formica rufibarbis</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma luxemburgense</i>	<i>Formica cunicularia</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma luxemburgense</i>	<i>Formica sanguinea</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma luxemburgense</i>	<i>Polyergus rufescens</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma michaeli</i>	<i>Formica obscuriventris</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma michaeli</i>	<i>Formica obscuripes</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma pergandei</i>	<i>Camponotus castaneus</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma pergandei</i>	<i>Formica integra</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma pergandei</i>	<i>Formica subsericea</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma petulans</i>	<i>Formica integra</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma petulans</i>	<i>Formica pergandei</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma petulans</i>	<i>Formica rubicunda</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma petulans</i>	<i>Formica subintegra</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma petulans</i>	<i>Formica subsericea</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Braconidae	<i>Elasmosoma petulans</i>	<i>Formica sanguinea</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma petulans</i>	<i>Formica opaciventris</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma schwarzi</i>	<i>Formica schaufussi</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma schwarzi</i>	<i>Polyergus lucidus</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma sp.</i>	<i>Formica obscuriventris</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma vigilans</i>	<i>Formica</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma vigilans</i>	<i>Formica perpilosa</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosoma vigilans</i>	<i>Formica subpolita</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Elasmosomites primordialis</i>	<i>Lasius sp.</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Kollasmosoma marikovskii</i>	<i>Formica pratensis</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Kollasmosoma platamonense</i>	<i>Cataglyphis bicolor</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Kollasmosoma platamonense</i>	<i>Messor semirufus</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Kollasmosoma sentum</i>	<i>Cataglyphis ibericus</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Neoneurus auctus</i>	<i>Formica pratensis</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Neoneurus auctus</i>	<i>Formica rufa</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Neoneurus auctus</i>	<i>Formica aquilonia</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Neoneurus clypeatus</i>	<i>Formica rufa</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Neoneurus clypeatus</i>	<i>Formica rufa</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Neoneurus mantis</i>	<i>Formica podzolica</i>	B	1	Dir.	Ex
Hymenoptera	Braconidae	<i>Neoneurus mantis</i>	<i>Formica podzolica</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Braconidae	<i>Neoneurus vesculus</i>	<i>Formica cunicularia</i>	B	1	Dir.	Ex
Hymenoptera	Chalcididae	<i>Smicromorpha doddi</i>	<i>Oecophylla smaragdina</i>	B	1	Dir.	Ex
Hymenoptera	Chalcididae	<i>Smicromorpha keralensis</i>	<i>Oecophylla smaragdina</i>	B	1	Dir.	Ex
Hymenoptera	Chalcididae	<i>Smicromorpha lagynos</i>	<i>Oecophylla smaragdina</i>	B	1	Dir.	Ex
Hymenoptera	Chalcididae	<i>Smicromorpha masneri</i>	<i>Oecophylla smaragdina</i>	B	1	Dir.	Ex
Hymenoptera	Chalcididae	<i>Smicromorpha minera</i>	<i>Oecophylla smaragdina</i>	B	1	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp.</i>	<i>Cyphomyrmex salvini</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp.</i>	<i>Trachymyrmex cf. zeteki</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp. 1</i>	<i>Cyphomyrmex transversus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp. 1</i>	<i>Cyphomyrmex rimosus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp. 1</i>	<i>Cyphomyrmex minutus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp. 2</i>	<i>Cyphomyrmex transversus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp. 2</i>	<i>Cyphomyrmex rimosus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp. 3</i>	<i>Cyphomyrmex transversus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp. 3</i>	<i>Cyphomyrmex rimosus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp. 4</i>	<i>Cyphomyrmex transversus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp. 4</i>	<i>Cyphomyrmex rimosus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp. 5</i>	<i>Cyphomyrmex transversus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp. 5</i>	<i>Cyphomyrmex minutus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp. 6</i>	<i>Cyphomyrmex transversus</i>	B	Ind.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Diapriidae	<i>Acanthopria sp. 7</i>	<i>Cyphomyrmex transversus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Acanthopria sp. 8</i>	<i>Cyphomyrmex transversus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Bruchopria hexatoma</i>	<i>Acromyrmex lundii</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Bruchopria hexatoma</i>	<i>Solenopsis richteri</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Bruchopria pentatoma</i>	<i>Solenopsis richteri</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Doliopria collegii</i>	<i>Eciton burchelli</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Doliopria collegii</i>	<i>Eciton quadriglume</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Doliopria myrmecobia</i>	<i>Acromyrmex lundii</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Mimopriella sp.</i>	<i>Cyphomyrmex rimosus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Mimopriella sp. 1</i>	<i>Trachymyrmex cf. zeteki</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Mimopriella sp. 2</i>	<i>Trachymyrmex cf. zeteki</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Oxypria sp.</i>	<i>Trachymyrmex cf. zeteki</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Plagiopria passerai</i>	<i>Plagiolepis pygmaea</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Szelenyopria lucens</i>	<i>Acromyrmex ambiguus</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Szelenyopria pampeana</i>	<i>Acromyrmex lobicornis</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Szelenyopria reichenspergeri</i>	<i>Eciton quadriglume</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Szelenyopria reichenspergeri</i>	<i>Neivamyrmex legionis</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Szelenyopria sp. 1</i>	<i>Trachymyrmex cf. zeteki</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Szelenyopria sp. 2</i>	<i>Trachymyrmex cf. zeteki</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Szelenyopria talitae</i>	<i>Acromyrmex subterraneus</i>	B	Ind.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species				
				Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Diapriidae	<i>Trichopria formicans</i>	<i>Acromyrmex lobicornis</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Trichopria myrmecophila</i>	<i>Solenopsis richteri</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Trichopria sp.</i>	<i>Acromyrmex lobicornis</i>	B	Ind.	Dir.	Ex
Hymenoptera	Diapriidae	<i>Trichopria sp.</i>	<i>Linepithema humile</i>	B	Ind.	Dir.	Ex
Hymenoptera	Encyrtidae	<i>Blanchardiscus pollux</i>	<i>Neoponera goeldii</i>	B	2	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Ancylotropus manipurensis</i>	<i>Camponotus sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Ancylotropus sp.</i>	<i>Odontomachus troglodytes</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Athairocharis vannoorti</i>	<i>Anoplolepis sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Austeucharis fasciiventris</i>	<i>Myrmecia gulosa</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Austeucharis fasciiventris</i>	<i>Myrmecia forficata</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Austeucharis implexa</i>	<i>Myrmecia pilosula</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Austeucharis myrmeciae</i>	<i>Myrmecia forficata</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Austeucharis myrmeciae</i>	<i>Myrmecia forficata</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Austeucharis sp.</i>	<i>Myrmecia nigriceps</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Austeucharis sp.</i>	<i>Myrmecia pavidia</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Austeucharis sp.</i>	<i>Myrmecia pilosula</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Austeucharis sp.</i>	<i>Myrmecia pyriformis</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Austeucharis sp.</i>	<i>Myrmecia tarsata</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Austeucharis sp.</i>	<i>Myrmecia vInd.ex</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Chalcura affinis</i>	<i>Odontomachus ruficeps</i>	B	Mult.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Eucharitidae	<i>Chalcura affinis</i>	<i>Myrmecia</i> sp.	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Chalcura deprivata</i>	<i>Odontomachus haematodes</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Chalcura nigricyanea</i>	<i>Rhytidoponera metallica</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Chalcura polita</i>	<i>Rhytidoponera metallica</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Chalcura</i> sp.	<i>Formica rufa</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Chalcura</i> sp. nr. <i>polita</i>	<i>Rhytidoponera chalybaea</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Dicoelothorax platycerus</i>	<i>Ectatomma brunneum</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Dilocantha lachaudii</i>	<i>Ectatomma tuberculatum</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis adscendens</i>	<i>Formica cunicularia</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis adscendens</i>	<i>Messor barbarus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis adscendens</i>	<i>Formica</i> sp.	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis adscendens</i>	<i>Formica rufa</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis bedeli</i>	<i>Cataglyphis bicolor</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis bedeli</i>	<i>Cataglyphis viaticus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis bedeli</i>	<i>Formica rufa</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis bedeli</i>	<i>Myrmecocystus viaticus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis bytinskisalzi</i>	<i>Cataglyphis bicolor</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis esakii</i>	<i>Formica fusca japonica</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis esakii</i>	<i>Formica</i> sp.	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis microcephala</i>	<i>Cataglyphis bicolor modus</i>	B	Mult.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species				
				Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Eucharitidae	<i>Eucharis punctata</i>	<i>Messor barbarus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis punctata</i>	<i>Messor concolor</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis punctata</i>	<i>Messor sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis shestakovi</i>	<i>Messor structor</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis sp.</i>	<i>Formica neorufibarbis</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Eucharis sp.</i>	<i>Myrmica incompleta</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Galearia coleopteroides</i>	<i>Pogonomyrmex carnivora</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Galearia latreillei</i>	<i>Ectatomma brunneum</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Galearia latreillei</i>	<i>Pogonomyrmex carnivora</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Gollumiella longipetiolata</i>	<i>Paratrechina sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Hydrorhoa sp. striaticeps</i> Kieffer complex	<i>Camponotus maculatus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Isomerala azteca</i>	<i>Ectatomma ruidum</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Isomerala coronata</i>	<i>Ectatomma ruidum</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Isomerala coronata</i>	<i>Ectatomma tuberculatum</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala atrata</i>	<i>Pachycondyla harpax</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala cuprea</i>	<i>Pachycondyla crassinoda</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala floridana</i>	<i>Pogonomyrmex badius</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala iridicolor</i>	<i>Ectatomma ruidum</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala iridicolor</i>	<i>Pachycondyla stigma</i>	B	Mult.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Eucharitidae	<i>Kapala iridicolor</i>	<i>Gnamptogenys regularis</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala iridicolor</i>	<i>Gnamptogenys striatula</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala iridicolor</i>	<i>Gnamptogenys sulcata</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala izapa</i>	<i>Ectatomma ruidum</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Gnamptogenys tortuolosa</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Odontomachus haematodus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Odontomachus hastatus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Odontomachus mayi</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Pachycondyla verenae</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Pachycondyla stigma</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Pachycondyla harpax</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Dinoponera lucida</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Gnamptogenys sulcata</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Hypoponera nitidula</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Odontomachus bauri</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Odontomachus brunneus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Odontomachus insularis</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Odontomachus laticeps</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Odontomachus meinerti</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Odontomachus opaciventris</i>	B	Mult.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Pachycondyla apicalis</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp.</i>	<i>Typhlomyrmex rogenhoferi</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp. 1</i>	<i>Ectatomma brunneum</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sp. 2</i>	<i>Ectatomma tuberculatum</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala sulcifacies</i>	<i>Ectatomma ruidum</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Kapala terminalis</i>	<i>Odontomachus haematodes insularis</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Latina rugosa</i>	<i>Odontomachus chelifer</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Lophyrocera variabilis</i>	<i>Camponotus sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Mateucharis rugulosa</i>	<i>Camponotus sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Neolosbanus gemma</i>	<i>Hypoconera sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Neolosbanus palgravei</i>	<i>Hypoconera sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Obeza floridana</i>	<i>Camponotus abdominalis</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Obeza floridana</i>	<i>Camponotus floridanus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema aenea</i>	<i>Solenopsis quinquecuspis</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema argentina</i>	<i>Pheidole nitidula</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema assectator</i>	<i>Pheidole sp.</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema coloradensis</i>	<i>Formica oreas comptula</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema coloradensis</i>	<i>Formica subnitens</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema coloradensis</i>	<i>Pheidole bicarinata</i>	B	Ind.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Eucharitidae	<i>Orasema coloradensis</i>	<i>Solenopsis molesta</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema costaricensis</i>	<i>Pheidole flavens</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema costaricensis</i>	<i>Pheidole vallifica</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema fraudulenta</i>	<i>Pheidole megacephala</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema minuta</i>	<i>Leptothorax allardycei</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema minuta</i>	<i>Pheidole nr. tetra</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema minuta</i>	<i>Pheidole sp.</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema minuta</i>	<i>Temnothorax allardycei</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema minutissima</i>	<i>Wasmannia auropunctata</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema minutissima</i>	<i>Wasmannia sigmoidea</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema monomoria</i>	<i>Monomorium sp.</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema occidentalis</i>	<i>Pheidole pilifera</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema pireta</i>	<i>Solenopsis sp.</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema rapo</i>	<i>Eciton quadriglume</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema robertsoni</i>	<i>Pheidole dentata</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema salebrosa</i>	<i>Solenopsis invicta</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema salebrosa</i>	<i>Solenopsis macdonaghi</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema salebrosa</i>	<i>Solenopsis richteri</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema simplex</i>	<i>Solenopsis invicta</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema simplex</i>	<i>Solenopsis quinquecuspis</i>	B	Ind.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Eucharitidae	<i>Orasema simplex</i>	<i>Solenopsis richteri</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema simplex</i>	<i>Solenopsis macdonaghi</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema simulatrix</i>	<i>Pheidole desertorum</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sixaolae</i>	<i>Solenopsis tenuis</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp.</i>	<i>Pheidole bilimeki</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp.</i>	<i>Pheidole paiute</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp.</i>	<i>Solenopsis invicta</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp.</i>	<i>Solenopsis sp.</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp.</i>	<i>Solenopsis xyloni</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp.</i>	<i>Tetramorium sp.</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp. b1 nr bakeri</i>	<i>Solenopsis geminata</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp. b1 nr bakeri</i>	<i>Solenopsis xyloni</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp. b2 nr bakeri</i>	<i>Pheidole nr californica</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp. b2 nr bakeri</i>	<i>Pheidole nr clementensis</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp. c1 near costari.</i>	<i>Pheidole dentata</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp. nr coloradensis</i>	<i>Formica oreas comptula</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp. nr. bouceki</i>	<i>Pheidole sp.</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp. uichancoi-group</i>	<i>Pheidole sp.</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema sp.1</i>	<i>Pheidole dentata</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema susanae</i>	<i>Pheidole nr. tetra</i>	B	Ind.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Eucharitidae	<i>Orasema susanae</i>	<i>Pheidole sp.</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema tolteca</i>	<i>Pheidole hirtula</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema tolteca</i>	<i>Pheidole sp.</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema tolteca</i>	<i>Pheidole vasliti car. alcoholua</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema valgius</i>	<i>Pheidole sp.</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema viridis</i>	<i>Pheidole dentata</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema viridis</i>	<i>Pheidole instabilis</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema wheeleri</i>	<i>Pheidole carbonaria</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema wheeleri</i>	<i>Pheidole ceres</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema wheeleri</i>	<i>Pheidole dentata</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema wheeleri</i>	<i>Pheidole kingi instabilis</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema wheeleri</i>	<i>Pheidole sciophila</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema wheeleri</i>	<i>Pheidole tepicana</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema worcesteri</i>	<i>Pheidole nitudula</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema worcesteri</i>	<i>Pheidole radoszkowski</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema xanthopus</i>	<i>Solenopsis quinquecuspis</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema xanthopus</i>	<i>Solenopsis daguerrei</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema xanthopus</i>	<i>Solenopsis saevissima</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema xanthopus</i>	<i>Solenopsis invicta</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasema xanthopus</i>	<i>Solenopsis richteri</i>	B	Ind.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Eucharitidae	<i>Orasemorpha eribotes</i>	<i>Pheidole sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasemorpha myrmicae</i>	<i>Pheidole sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasemorpha tridentata</i>	<i>Pheidole proxima</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Orasemorpha xeniades</i>	<i>Pheidole tasmaniensis</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Pogonocharis browni</i>	<i>Gnamptogenys menadensis</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Pseudochalcura americana</i>	<i>Camponotus sp.</i>	B	2	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Pseudochalcura gibbosa</i>	<i>Camponotus novaeboracensis</i>	B	2	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Pseudochalcura nigrocyanea</i>	<i>Camponotus sp.</i>	B	2	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Pseudochalcura sculpturata</i>	<i>Camponotus planatus</i>	B	2	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Pseudometagea schwarzii</i>	<i>Lasius neoniger</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Pseudometagea schwarzii</i>	<i>Lasius sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Pseudometagea sp.</i>	<i>Lasius fuliginosus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Pseudometagea sp.</i>	<i>Lasius sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Rhipipalloidea madangensis</i>	<i>Camponotus sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Rhipipalloidea mira</i>	<i>Polyrhachis femorata</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Rhipipalloidea sp.</i>	<i>Camponotus sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Rhipipalloidea sp.</i>	<i>Polyrhachis sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Schizaspidia convergens</i>	<i>Odontomachus haematodes</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Schizaspidia diacammae</i>	<i>Diacamma scalpratum</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Schizaspidia nasua</i>	<i>Odontomachus rixosus</i>	B	Mult.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Eucharitidae	<i>Stilbula arenae</i>	<i>Polyrhachis sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Stilbula cyniformis</i>	<i>Camponotus aethiops</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Stilbula cyniformis</i>	<i>Camponotus aethiops</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Stilbula cyniformis</i>	<i>Camponotus japonicus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Stilbula cyniformis</i>	<i>Camponotus maculatus sanctus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Stilbula cyniformis</i>	<i>Camponotus marginatus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Stilbula cyniformis</i>	<i>Camponotus sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Stilbula cyniformis</i>	<i>Rhytidoponera violacea</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Stilbula cyniformis tenuicornis</i>	<i>Camponotus herculeanus japonicus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Stilbula cyniformis tenuicornis</i>	<i>Camponotus lingiperda obscuripes</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Stilbula polyrachicida</i>	<i>Polyrhachis dives</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Stilbuloida calomyrmecis</i>	<i>Calomyrmex purpureus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Stilbuloida doddi</i>	<i>Camponotus sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Stilbuloida doddi</i>	<i>Polyrhachis dives</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Timioderus acuminatus</i>	<i>Pheidole capensis</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Tricoryna alcornis</i>	<i>Rhytidoponera violacea</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Tricoryna chalcoponerae</i>	<i>Rhytidoponera metallica</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Tricoryna chalcoponerae</i>	<i>Rhytidoponera victoriae</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Tricoryna ectatommae</i>	<i>Ectatomma sp.</i>	B	Mult.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Eucharitidae	<i>Tricoryna ectatommae</i>	<i>Rhytidoponera sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Tricoryna iello</i>	<i>Rhytidoponera sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Tricoryna minor</i>	<i>Rhytidoponera metallica</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Tricoryna minor</i>	<i>Rhytidoponera victoriae</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Tricoryna sp.</i>	<i>Rhytidoponera violacea</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Tricoryna sp. nr. alcicornis</i>	<i>Rhytidoponera violacea</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eucharitidae	<i>Zulucharis campbelli</i>	<i>Camponotus sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eulophidae	<i>Horismenus floridensis</i>	<i>Camponotus abdominalis</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eulophidae	<i>Horismenus floridensis</i>	<i>Camponotus atriceps</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eulophidae	<i>Horismenus floridensis</i>	<i>Camponotus floridanus</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eulophidae	<i>Horismenus myrmecophagus</i>	<i>Camponotus sp. ca. textor</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eulophidae	<i>Horismenus myrmecophagus</i>	<i>Camponotus sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eulophidae	<i>Horismenus sp.</i>	<i>Crematogaster acuta</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eulophidae	<i>Melittobia acasta</i>	<i>Formica fusca</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eulophidae	<i>Melittobia acasta</i>	<i>Formica pratensis</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eulophidae	<i>Melittobia acasta</i>	<i>Formica sanguinea</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eulophidae	<i>Melittobia australica</i>	<i>Crematogaster brevispinosa</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eulophidae	<i>Myrmokata diparoides</i>	<i>Crematogaster sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eulophidae	<i>Myrmokata sp.</i>	<i>Crematogaster sp.</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eulophidae	<i>Pediobius marjorae</i>	<i>Lepisiota sp.</i>	B	Mult.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Eupelmidae	<i>Anastatus myrmecobius</i>	<i>Temnothorax purpurata</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eupelmidae	<i>Anastatus reduvii</i>	<i>Pseudomyrmex elongata</i>	B	Mult.	Dir.	Ex
Hymenoptera	Eurytomidae	<i>Aximopsis affinis</i>	<i>Azteca alfari</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eurytomidae	<i>Aximopsis affinis</i>	<i>Azteca pittieri</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eurytomidae	<i>Aximopsis affinis</i>	<i>Azteca sp.</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eurytomidae	<i>Aximopsis aztecicida</i>	<i>Azteca alfari</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eurytomidae	<i>Aximopsis aztecicida</i>	<i>Azteca constructor</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eurytomidae	<i>Aximopsis sp.</i>	<i>Azteca alfari</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eurytomidae	<i>Aximopsis sp.</i>	<i>Azteca australis</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eurytomidae	<i>Aximopsis sp.</i>	<i>Azteca ovaticeps</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eurytomidae	<i>Aximopsis sp.</i>	<i>Azteca salti</i>	B	Ind.	Dir.	Ex
Hymenoptera	Eurytomidae	<i>Aximopsis sp.</i>	<i>Camponotus balzani</i>	B	Ind.	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Eurypterna cremieri</i>	<i>Lasius nipponensis</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Eurypterna cremieri</i>	<i>Lasius fuliginosus</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Eurypterna cremieri</i>	<i>Formica rufa</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Ghilaromma fuliginosi</i>	<i>Lasius fuliginosus</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon arakawae</i>	<i>Lasius fuliginosus</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Lasius flavus</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Lasius affinis</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Lasius brunneus</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Myrmica scabrinodis</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Formica rufa</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Formica rufibarbis</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Formica sanguinea</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Lasius alienus</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Lasius brunneus</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Lasius flavus</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Lasius grandis</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Lasius niger</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Myrmica lobicornis</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Myrmica ruginodis</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Tapinoma erraticum</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Formica rufibarbis</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Formica sanguinea</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Lasius niger</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Myrmica scabrinodis</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon buccatus</i>	<i>Tapinoma erraticum</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon cremieri</i>	<i>Formica fuliginosa</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon cremieri</i>	<i>Lasius fuliginosus</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon cremieri</i>	<i>Formica rufa</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Hymenoptera	Ichneumonidae	<i>Hybrizon cremieri</i>	<i>Lasius fuliginosus</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon cremieri</i>	<i>Lasius fuliginosus</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hybrizon rileyi</i>	<i>Lasius alienus</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Hyrbizon fuliginosi</i>	<i>Lasius fuliginosus</i>	B	1	Dir.	Ex
Hymenoptera	Ichneumonidae	<i>Sp. nov.</i>	<i>Myrmica kotokui</i>	B	1	Dir.	Ex
Hymenoptera	Mutillidae	<i>Ponerotilla clarki</i>	<i>Brachyponera lutea</i>	B	Ind.	Dir.	Ex
Hymenoptera	Mutillidae	<i>Ponerotilla crinata</i>	<i>Brachyponera lutea</i>	B	Ind.	Dir.	Ex
Hymenoptera	Mutillidae	<i>Ponerotilla incarinata</i>	<i>Brachyponera lutea</i>	B	Ind.	Dir.	Ex
Hymenoptera	Mutillidae	<i>Ponerotilla lamelligera</i>	<i>Brachyponera lutea</i>	B	Ind.	Dir.	Ex
Hymenoptera	Mutillidae	<i>Ponerotilla lissantyx</i>	<i>Brachyponera lutea</i>	B	Ind.	Dir.	Ex
Hymenoptera	Pteromalidae	<i>Pheidoloxenus wheeleri</i>	<i>Pheidole ceres</i>	B	Unk.	Dir.	Ex
Hymenoptera	Pteromalidae	<i>Pheidoloxenus wheeleri</i>	<i>Pheidole instabilis</i>	B	Unk.	Dir.	Ex
Diptera	Chloropidae	<i>Pseudogaurax paratolmos</i>	<i>Apterostigma dentigerum</i>	B	Unk.	Dir.	Ex
Diptera	Ephydriidae	<i>Rhynchopsilopa nitidissima</i>	<i>Crematogaster sp.</i>	A	1	Dir.	Ex
Diptera	Ephydriidae	<i>Rhynchopsilopa laevigata</i>	<i>Crematogaster sp.</i>	A	1	Dir.	Ex
Diptera	Helosciomyzidae	<i>Heliosciomyza subalpina</i>	<i>Monomorium antarcticum</i>	B	Ind.	Dir.	Ex
Diptera	Phoridae	<i>Acanthophorides clavircercus</i>	<i>Eciton burchelli</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Acanthophorides condei</i>	<i>Eciton burchelli</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Acanthophorides divergens</i>	<i>Eciton burchelli</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Acanthophorides labidophilus</i>	<i>Labidus praedator</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Acanthophorides longicornis</i>	<i>Labidus praedator</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Acanthophorides pilosicauda</i>	<i>Labidus praedator</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Aenigmatias brevifrons</i>	<i>Formica rufibarbis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Aenigmatias dorni</i>	<i>Formica glebaria</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Aenigmatias dorni</i>	<i>Formica rufibarbis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Aenigmatias franzi</i>	<i>Lasius niger</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Aenigmatias franzi</i>	<i>Myrmica ruginodis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Aenigmatias lubbocki</i>	<i>Formica exsecta</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Aenigmatias lubbocki</i>	<i>Formica fusca</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Aenigmatias lubbocki</i>	<i>Formica picea</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Aenigmatias lubbocki</i>	<i>Formica rufibarbis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Aenigmatias lubbocki</i>	<i>Formica sanguinea</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Aenigmatias lubbocki</i>	<i>Formica transcaucasica</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Allochaeta excedens</i>	<i>Atta laevigata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Allochaeta excedens</i>	<i>Atta sexdens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Allochaeta longiciliata</i>	<i>Acromyrmex niger</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Allochaeta longiciliata</i>	<i>Acromyrmex Mult. icinodus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Allochaeta muticinodus</i>	<i>Acromyrmex niger</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Allochaeta wallerae</i>	<i>Atta cephalotes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus analis</i>	<i>Labidus coecus</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Apocephalus angustinervis</i>	<i>Camponotus rufipes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus asymmetricus</i>	<i>Atta cephalotes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus asyndetus</i>	<i>Gnamptogenys bispinosa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus atrimarginatus</i>	<i>Pachycondyla unidentata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus atrimarginatus</i>	<i>Odontomachus bauri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus atrimarginatus</i>	<i>Odontomachus laticeps</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus attophilus</i>	<i>Atta laevigata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus attophilus</i>	<i>Atta sexdens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus attophilus</i>	<i>Atta cephalotes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus attophilus</i>	<i>Atta bisphaerica</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus attophilus</i>	<i>Atta colombica</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus augustinervis</i>	<i>Camponotus rufipes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus azteca</i>	<i>Azteca sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus barbicauda</i>	<i>Acromyrmex lundii</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus barbiventris</i>	<i>Odontomachus bauri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus bispinosus</i>	<i>Camponotus cingulatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus brevifrons</i>	<i>Gnamptogenys sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus brochus</i>	<i>Camponotus banghassi</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus brochus</i>	<i>Camponotus rapax</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus brunneiventris</i>	<i>Pheidole hyatti</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Apocephalus brunneiventris</i>	<i>Pheidole perpilosa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus camponoti</i>	<i>Camponotus rufipes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus cantleyi</i>	<i>Acromyrmex sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus catholicus</i>	<i>Odontomachus bauri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus catholicus</i>	<i>Odontomachus chelifer</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus catholicus</i>	<i>Pachycondyla crassinoda</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus catholicus</i>	<i>Pachycondyla impressa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus catholicus</i>	<i>Odontomachus hastatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus catholicus</i>	<i>Odontomachus laticeps</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus catholicus</i>	<i>Pachycondyla harpax</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus catholicus</i>	<i>Cephalotes atatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus catholicus</i>	<i>Dolichoderus attelaboides</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus catholicus</i>	<i>Ectatomma gonion</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus collatus</i>	<i>Pachycondyla impressa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus colombicus</i>	<i>Atta colombica</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus comatus</i>	<i>Labidus coecus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus comosus</i>	<i>Ectatomma tuberculatum</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus comosus</i>	<i>Odontomachus laticeps</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus concisus</i>	<i>Camponotus pennsylvanicus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus conecitonis</i>	<i>Eciton lucanoides</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Apocephalus constrictus</i>	<i>Pachycondyla apicalis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus constrictus</i>	<i>Pachycondyla impressa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus constrictus</i>	<i>Pachycondyla unidentata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus constrictus</i>	<i>Pachycondyla villosa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus contortiventris</i>	<i>Pachycondyla impressa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus coquilletti</i>	<i>Camponotus ferrugineus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus coquilletti</i>	<i>Camponotus maculatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus coquilletti</i>	<i>Camponotus pennsylvanicus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus coquilletti</i>	<i>Camponotus sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus coquilletti</i>	<i>Camponotus sansabeanus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus crassilatus</i>	<i>Pachycondyla unidentata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus crassilatus</i>	<i>Pachycondyla impressa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus crassilatus</i>	<i>Pachycondyla villosa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus crassilatus</i>	<i>Pachycondyla apicalis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus crucicauda</i>	<i>Camponotus crassus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus crucicauda</i>	<i>Camponotus sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus cultellatus</i>	<i>Eciton burchelli</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus cultellatus</i>	<i>Eciton vagans</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus deceptus</i>	<i>Pachycondyla commutata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus densepilosus</i>	<i>Pachycondyla crassinoda</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Apocephalus dinoponeræ</i>	<i>Dinoponera longipes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus dubiatus</i>	<i>Acromyrmex subterraneus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus ecitonis</i>	<i>Labidus praedator</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus elizaldæ</i>	<i>Camponotus cingulatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus emargilatus</i>	<i>Camponotus sericeiventris</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus eurydomus</i>	<i>Pachycondyla harpax</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus exlucida</i>	<i>Dinoponera lucida</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus feeneri</i>	<i>Pheidole dentata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus gigantivorus</i>	<i>Dinoponera gigantea</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus glabriventris</i>	<i>Ectatomma ruidum</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus globosus</i>	<i>Pachycondyla villosa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus grandipalpus</i> sp.	<i>Pheidole</i> sp.	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus horridus</i>	<i>Camponotus vicinus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus infradentatus</i>	<i>Nomamyrmex esenbecki</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus inimicus</i>	<i>Labidus coecus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus kungæ</i>	<i>Dinoponera longipes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus laceyi</i>	<i>Camponotus femoratus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus lamellatus</i>	<i>Acromyrmex muticynoda</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus lamellatus</i>	<i>Acromyrmex niger</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus lanceatus</i>	<i>Camponotus rufipes</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Apocephalus latinsulosus</i>	<i>Pachycondyla impressa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus lobicauda</i>	<i>Ectatomma tuberculatum</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus lopesi</i>	<i>Odontomachus haematodus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus luteihalteratus</i>	<i>Acromyrmex coronatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus luteihalteratus</i>	<i>Acromyrmex lundii</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus luteihalteratus</i>	<i>Acromyrmex muticinodus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus luteihalteratus</i>	<i>Acromyrmex niger</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus luteihalteratus</i>	<i>Acromyrmex sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus magnicauda</i>	<i>Camponotus sericeiventris</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus melinus</i>	<i>Dolichoderus attelaboides</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus melinus</i>	<i>Dolichoderus decollatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus melinus</i>	<i>Pachycondyla commutata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus miricauda</i>	<i>Dinoponera gigantea</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus mucronatus</i>	<i>Camponotus blandus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus neivai</i>	<i>Acromyrmex sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus neivai</i>	<i>Acromyrmex heyeri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus neivai</i>	<i>Acromyrmex lundii</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus oergandei</i>	<i>Camponotus pennsylvanicus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus onorei</i>	<i>Acromyrmex sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus orthocladus</i>	<i>Pheidole diversipilosa</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Apocephalus pachycondylae</i>	<i>Eciton lucanoides</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus paldiae</i>	<i>Odontomachus chelifer</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus paraponerae</i>	<i>Ectatomma tuberculatum</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus paraponerae</i>	<i>Paraponera clavata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus paraponerae</i>	<i>Dolichoderus attelaboides</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus paraponerae</i>	<i>Ectatomma lugens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus paraponerae</i>	<i>Ectatomma ruidum</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus paraponerae</i>	<i>Pachycondyla apicalis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus paraponerae</i>	<i>Pachycondyla commutata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus paraponerae</i>	<i>Pachycondyla crassinoda</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus paraponerae</i>	<i>Pachycondyla villosa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus pergandei</i>	<i>Camponotus pennsylvanicus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus persecutor</i>	<i>Nomamyrmex esenbecki</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus piliventris</i>	<i>Pachycondyla striata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus platypalpis</i>	<i>Labidus praedator</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus portalensis</i>	<i>Aphaenogaster texana</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus praedator</i>	<i>Labidus praedator</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus pseudocercus</i>	<i>Acromyrmex coronatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus quadriglumis</i>	<i>Eciton quadriglume</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus rionegrensis</i>	<i>Acromyrmex lundii</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Apocephalus rionegrensis</i>	<i>Acromyrmex subterraneus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus ritualis</i>	<i>Atta cephalotes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus roeschardae</i>	<i>Cephalotes atratus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus setitarsus</i>	<i>Atta vollenweideri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus setiventris</i>	<i>Camponotus crassus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus setiventris</i>	<i>Camponotus rufipes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus silvestrii</i>	<i>Iridomyrmex humile</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus similis</i>	<i>Camponotus sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus similis</i>	<i>Camponotus vicinus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus similis</i>	<i>Camponotus sansabeanus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus sp.</i>	<i>Atta cephalotes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus sp.</i>	<i>Daceton armigeron</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus sp.</i>	<i>Dinoponera australis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus sp.</i>	<i>Dolichoderus decollatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus sp.</i>	<i>Eciton burchelli</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus sp.</i>	<i>Labidus pradaetor</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus sp.</i>	<i>Pachycondyla harpax</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus sp.</i>	<i>Pheidole dentata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus sp.</i>	<i>Pheidole sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus sp.</i>	<i>Pheidole titanis</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Apocephalus sp. 21</i>	<i>Gnamptogenys bispinosa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus sp. 29</i>	<i>Pheidole subdentata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus sp. 84</i>	<i>Pachycondyla obscuricornis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus spinosus</i>	<i>Atta cephalotes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus stiventris</i>	<i>Camponotus crassus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus tanyurus</i>	<i>Paraponera clavata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus tenuipes</i>	<i>Pheidole dentata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus trifidus</i>	<i>Pachycondyla crassinoda</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus vicosae</i>	<i>Atta laevigata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus vicosae</i>	<i>Atta sexdens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus vicosae</i>	<i>Atta sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus vicosae</i>	<i>Atta vollenweideri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apocephalus wallerae</i>	<i>Atta texana</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apodicrania molinai</i>	<i>Camponotus rapax</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apodicrania molinai</i>	<i>Camponotus sericeiventris</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apodicrania sp.</i>	<i>Dinoponera longipes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apodicrania termitophila</i>	<i>Eciton hamatum</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apodicrania termitophila</i>	<i>Solenopsis invicta</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Apodicrania termitophila</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Auxanommatidia myrmecophila</i>	<i>Camponotus rufipes</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Beckerina sp.</i>	<i>Paraponera clavata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Borgmeieriphora greigae</i>	<i>Eciton sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Ceratoconus setipennis</i>	<i>Linepithema humile</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Conicera sp. A</i>	<i>Dorylus brevipennis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Conicera wittei</i>	<i>Leptogenys processionalis s. dis-tinguenda</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia adunca</i>	<i>Neivamyrmex texanus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia australis</i>	<i>Neivamyrmex diversinodis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia brasiliensis</i>	<i>Eciton schletendali</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia brasiliensis</i>	<i>Nomamyrmex esenbecki</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia brasiliensis</i>	<i>Nomamyrmex hartigi</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia costalis</i>	<i>Neivamyrmex legionis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia costalis</i>	<i>Neivamyrmex pseudops</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia crassispina</i>	<i>Nomamyrmex esenbecki</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia crassispina</i>	<i>Nomamyrmex hartigi</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia longipes</i>	<i>Labidus coecus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia pilosa</i>	<i>Eciton schletendali</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia pilosa</i>	<i>Nomamyrmex esenbecki</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia pilosa</i>	<i>Nomamyrmex hartigi</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia salesiana</i>	<i>Eciton schletendali</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Cremersia salesiana</i>	<i>Nomamyrmex hartigi</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia setitarsus</i>	<i>Labidus praedator</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia sp.</i>	<i>Nomamyrmex hartigii</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia sp.</i>	<i>Neivamyrmex nigrescens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia sp.</i>	<i>Neivamyrmex pilosus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia spinicosta</i>	<i>Eciton coecum</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia spinicosta</i>	<i>Labidus coecus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia spinicosta</i>	<i>Nomamyrmex esenbecki</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Cremersia spinosissima</i>	<i>Labidus praedator</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Dacnophora legionis</i>	<i>Labidus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Dacnophora legionis</i>	<i>Neivamyrmex</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Dacnophora legionis</i>	<i>Neivamyrmex legionis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Dacnophora legionis</i>	<i>Neivamyrmex raptans</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Dacnophora pectinatus</i>	<i>Neivamyrmex nigrescens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Dacnophora setithorax</i>	<i>Labidus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Dacnophora setithorax</i>	<i>Neivamyrmex</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Dacnophora setitjorax</i>	<i>Labidus coecus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Dacnophora sp.</i>	<i>Labidus praedator</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora appretiata</i>	<i>Camponotus sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora appretiata</i>	<i>Eciton burchelli</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Diocophora appretiata</i>	<i>Eciton quadriglume</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora disparifrons</i>	<i>Camponotus cingulatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora disparifrons</i>	<i>Camponotus cingulatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora disparifrons</i>	<i>Camponotus crassus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora disparifrons</i>	<i>Camponotus crassus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora disparifrons</i>	<i>Camponotus rufipes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora disparifrons</i>	<i>Camponotus rufipes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora disparifrons</i>	<i>Camponotus sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora disparifrons</i>	<i>Eciton burchelli</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora disparifrons</i>	<i>Nomamyrmex esenbecki</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora duplexseta</i>	<i>Eciton lucanoides</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora modesta</i>	<i>Camponotus rufipes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora sp.</i>	<i>Camponotus banghaasi</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora sp.</i>	<i>Camponotus femoratus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora sp.</i>	<i>Camponotus rapax</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora sp.</i>	<i>Camponotus sericeiventris</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora sp.</i>	<i>Cephalotes atratus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora sp.</i>	<i>Dolichoderus attelaboides</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora sp.</i>	<i>Dolichoderus bispinosus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora sp.</i>	<i>Dolichoderus decollatus</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Diocophora sp.</i>	<i>Eciton hamatum</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Diocophora trichogaster</i>	<i>Camponotus floridanus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Eibesfeldtphora attae</i>	<i>Atta cephalotes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Eibesfeldtphora breviloba</i>	<i>Atta robusta</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Eibesfeldtphora digitata</i>	<i>Atta robusta</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Eibesfeldtphora mexicanae</i>	<i>Atta mexicana</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Eibesfeldtphora pala</i>	<i>Atta cephalotes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Eibesfeldtphora pala</i>	<i>Atta colombica</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Eibesfeldtphora prolixa</i>	<i>Atta cephalotes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Eibesfeldtphora tonhascai</i>	<i>Atta laevigata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Eibesfeldtphora tonhascai</i>	<i>Atta sexdens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Eibesfeldtphora trifurcata</i>	<i>Atta sexdens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Eibesfeldtphora trilobata</i>	<i>Atta vollenweideri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Epactoselia provallaris</i>	<i>Crematogaster sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Iridophora clarki</i>	<i>Carebara</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Iridophora clarki</i>	<i>Iridomyrmex cordatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia aurea</i>	<i>Eciton burchelli</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia aurea</i>	<i>Paraponera clavata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia enderleini</i>	<i>Eciton burchelli</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia furvicolor</i>	<i>Dorylus brevipennis</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Megaselia holosericea</i>	<i>Camponotus holosericus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia holosericea</i>	<i>Polyrhachis bellicosa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia holosericea</i>	<i>Polyrhachis illaudata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia insignicauda</i>	<i>Leptogenys mutabilis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia kodongi</i>	<i>Pheidologeton sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia pagei</i>	<i>Odontomachus simillimus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia persecutrix</i>	<i>Camponotus gigas</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sembeli</i>	<i>Iridomyrmex cordatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Atta texana</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Camponotus holosericus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Camponotus sericeiventris</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Cephalotes atratus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Dolichoderus attelaboides</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Dolichoderus bispinosus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Dolichoderus lugens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Eciton burchelli</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Ectatomma tuberculatum</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Odontomachus bauri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Odontomachus laticeps</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Pachycondyla commutata</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Pachycondyla impressa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Pachycondyla unidentata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Paraponera clavata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Polyrhachis bellicosa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp.</i>	<i>Neivamyrmex opacithorax</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp. A</i>	<i>Dinoponera lucida</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp. B</i>	<i>Dinoponera lucida</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp. Q</i>	<i>Dorylus nigricans</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Megaselia sp. R</i>	<i>Dorylus nigricans</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Menoziola schmitzi</i>	<i>Camponotus herculanus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Menoziola schmitzi</i>	<i>Crematogaster scutellaris</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Microselia deemingi</i>	<i>Camponotus acvapimensis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Microselia rivierae</i>	<i>Camponotus cruentatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Microselia southwoodi</i>	<i>Camponotus vagus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Microselia texana</i>	<i>Paratrechina melanderi</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Microselia texana</i>	<i>Pheidole constipata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius biarticulatus</i>	<i>Labidus praedator</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius brandaoi</i>	<i>Atta vollenweideri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius brandaoi</i>	<i>Atta vollenweideri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius catharinensis</i>	<i>Acromyrmex lundii</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Myrmosicarius catharinensis</i>	<i>Acromyrmex heyeri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius cristobalensis</i>	<i>Acromyrmex lobicornis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius crudelis</i>	<i>Atta sexdens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius crudelis</i>	<i>Acromyrmex crassipinus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius cuspidatus</i>	<i>Acromyrmex niger</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius cuspidatus</i>	<i>Acromyrmex muticinodus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius cuspidatus</i>	<i>Acromyrmex subterraneus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius exrobusta</i>	<i>Atta robusta</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius gonzalezae</i>	<i>Atta vollenweideri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius gonzalezae</i>	<i>Atta vollenweideri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius gracilipes</i>	<i>Acromyrmex subterraneus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius grandicornis</i>	<i>Atta sexdens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius grandicornis</i>	<i>Atta bisphaerica</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius grandicornis</i>	<i>Eciton coecum</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius grandicornis</i>	<i>Labidus coecus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius grandicornis</i>	<i>Nomamyrmex esenbecki</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius grandicornis</i>	<i>Nomamyrmex esenbecki</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius infestans</i>	<i>Acromyrmex aspersus mesonotalis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius infestans</i>	<i>Acromyrmex disciger</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius infestans</i>	<i>Acromyrmex subterraneus</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Myrmosicarius longipalpis</i>	<i>Acromyrmex hispidus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius persecutor</i>	<i>Acromyrmex lundi</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius tarsipennis</i>	<i>Acromyrmex niger</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius tarsipennis</i>	<i>Acromyrmex muticinodus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Myrmosicarius texanus</i>	<i>Atta texana</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora acromyrmecis</i>	<i>Acromyrmex sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora acromyrmecis</i>	<i>Atta sexdens rubropilosa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora acromyrmecis</i>	<i>Acromyrmex disciger</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora acromyrmecis</i>	<i>Atta sexdens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora curvinervis</i>	<i>Atta sexdens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora curvinervis</i>	<i>Atta cephalotes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora declinata</i>	<i>Atta laevigata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora declinata</i>	<i>Atta sexdens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora declinata</i>	<i>A. sexdens rubropilosa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora declinata</i>	<i>Atta sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora elongata</i>	<i>A. sexdens rubropilosa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora erthali</i>	<i>Atta laevigata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora sp.</i>	<i>Atta mexicana</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora sp. 1</i>	<i>Atta cephalotes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohniphora sp. 2</i>	<i>Atta cephalotes</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Neodohrniphora tonhascai</i>	<i>A. sexdens rubropilosa</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Neodohrniphora bragancai</i>	<i>Atta bisphaerica</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Nothomicrodon aztecarum</i>	<i>Azteca trigona</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Nothomicrodon sp.</i>	<i>Azteca chartifex</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Procliniella hostilis</i>	<i>Acromyrmex niger</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Procliniella hostilis</i>	<i>Acromyrmex muticinodus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon aduncus</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon affinis</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon amuletum</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon amuletum</i>	<i>Solenopsis xyloni</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon andinus</i>	<i>Solenopsis electra</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon andinus</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon annulus</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon antiguensis</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon antiguensis</i>	<i>Solenopsis xyloni</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon arcuatus</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon bifidus</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon bispinosus</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon borgmeieri</i>	<i>Camponotus cingulatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon borgmeieri</i>	<i>Camponotus rufipes</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Pseudacteon borgmeieri</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon brevicauda</i>	<i>Myrmica ruginodis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon brevicauda</i>	<i>Myrmica scabrinodis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon browni</i>	<i>Neivamyrmex adnepos</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon browni</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon bulbosus</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon calderensis</i>	<i>Solenopsis interrupta</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon calderensis</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon californiensis</i>	<i>Liometopum occidentale</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon comatus</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon conicornis</i>	<i>Solenopsis sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon convexicauda</i>	<i>Paratrechina fulva</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon convexicauda</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon crawfordi</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon crawfordi</i>	<i>Solenopsis xyloni</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon crawfordi</i>	<i>Solenopsis aurea</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon crawfordi</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon cultellatus</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon curvatus</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon curvatus</i>	<i>Solenopsis richteri</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Pseudacteon curvatus</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon curvatus</i>	<i>Solenopsis invicta</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon curvatus</i>	<i>Solenopsis spp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon deltoides</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon dentiger</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon disneyi</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon dorymyrmecis</i>	<i>Dorymyrmex pyramicus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon formicarum</i>	<i>Tapinoma erraticum</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon formicarum</i>	<i>Formica sanguinea</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon formicarum</i>	<i>Lasius alienus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon formicarum</i>	<i>Lasius emarginatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon formicarum</i>	<i>Lasius flavus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon formicarum</i>	<i>Lasius fuliginosus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon formicarum</i>	<i>Lasius niger</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon formicarum</i>	<i>Lasius umbratus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon formicarum</i>	<i>Myrmica lobicornis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon fowleri</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon fowleri</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon genebrae</i>	<i>Linepithema sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon gracilisetus</i>	<i>Nylanderia arenivaga</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species				
				Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Pseudacteon grandis</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon hippeus</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon kungae</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon laticarinatus</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon lenkoi</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon litoralis</i>	<i>Solenopsis invicta</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon litoralis</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon litoralis</i>	<i>Solenopsis richteri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon litoralis</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon lonicauda</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon lontrae</i>	<i>Linepithema sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon nocens</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon nudicornis</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon obtusus</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon obtusus</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon obtusus</i>	<i>Solenopsis invicta</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon obtusus</i>	<i>Solenopsis richteri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon onyx</i>	<i>Crematogaster lineolata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon onyx</i>	<i>Crematogaster sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon palomita</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Pseudacteon pradei</i>	<i>Solenopsis invicta</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon pradei</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon pusillus</i>	<i>Linepithema sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon pusillus</i>	<i>Iridomyrmex humile</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon quinni</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon robustus</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon simplex</i>	<i>Neivamyrmex pilosus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon solenopsidis</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon solenopsidis</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon sp.</i>	<i>Crematogaster parabiatica</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon sp.</i>	<i>Pachycondyla sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon sp.</i>	<i>Pseudolasius sp.</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon spatulatus</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon spatulatus</i>	<i>Solenopsis xyloni</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon spp.</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon tricuspis</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon tricuspis</i>	<i>Solenopsis richteri</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon tricuspis</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon tricuspis</i>	<i>Solenopsis invicta</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon wasmanni</i>	<i>Solenopsis invicta</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Pseudacteon wasmanni</i>	<i>Solenopsis geminata</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudacteon wasmanni</i>	<i>Solenopsis saevissima</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Pseudogaurax paratolmos</i>	<i>Apterostigma dentigerum</i>	B	Mult.	Dir.	Ex
Diptera	Phoridae	<i>Pseudogaurax paratolmos</i>	<i>Apterostigma dentigerum</i>	B	Mult.	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia conica</i>	<i>Camponotus pennsylvanicus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia conica</i>	<i>Dolichoderus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia gymnopleura</i>	<i>Acromyrmex</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia gymnopleura</i>	<i>Acropyga</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia gymnopleura</i>	<i>Camponotus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia gymnopleura</i>	<i>Camponotus rufipes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia gymnopleura</i>	<i>Dolichoderus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia maculinea</i>	<i>Acromyrmex</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia maculinea</i>	<i>Acropyga</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia maculinea</i>	<i>Camponotus rapax</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia maculinea</i>	<i>Dolichoderus lugens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia maculinea</i>	<i>Camponotus sericeiventris</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia maculinea</i>	<i>Dolichoderus lugens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia nubilifurca</i>	<i>Camponotus sericeiventris</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia sp.</i>	<i>Camponotus abdominalis</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia sp.</i>	<i>Camponotus banghassi</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Rhyncophoromyia</i> sp.	<i>Camponotus femoratus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia</i> sp.	<i>Camponotus rapax</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia</i> sp.	<i>Camponotus sericeiventris</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia</i> sp.	<i>Dinoponera longipes</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia</i> sp.	<i>Dolichoderus bidens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia</i> sp.	<i>Dolichoderus bispinosus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia</i> sp.	<i>Dolichoderus decollatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia</i> sp.	<i>Dolichoderus lugens</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia</i> sp.	<i>Dolichoderus quadrideniculatus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia</i> sp.	<i>Dolichoderus</i> sp.	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia trivittata</i>	<i>Camponotus banghassi</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia trivittata</i>	<i>Camponotus rapax</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Rhyncophoromyia trivittata</i>	<i>Camponotus sericeiventris</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Sorowoodiphoragombahensis</i> sp.	<i>Euprenolepis procera</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Stenoneurellis laticeps</i>	<i>Acromyrmex niger</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Stenoneurellis laticeps</i>	<i>Acromyrmex muticinodus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Stethopathusa corporaali</i>	<i>Odontomachus rixosus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Styletta crocea</i>	<i>Eciton burchelli</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Trucidophora camponoti</i>	<i>Camponotus herculanus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Trucidophora camponoti</i>	<i>Camponotus novaeboracensis</i>	B	1	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Diptera	Phoridae	<i>Trucidophora camponoti</i>	<i>Camponotus pennsylvanicus</i>	B	1	Dir.	Ex
Diptera	Phoridae	<i>Trucidophora feldhaarae</i>	<i>Crematogaster</i> sp.	B	1	Dir.	Ex
Diptera	Syrphidae	<i>Hypselosyrphus trigonus</i>	<i>Neoponera villosa</i>	B	Ind.	Dir.	Ex
Diptera	Tachinidae	<i>Strongylogaster globula</i>	<i>Lasius alienus</i>	B	1	Dir.	Ex
Diptera	Tachinidae	<i>Strongylogaster globula</i>	<i>Lasius niger</i>	B	1	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Caenocholax fenyesei</i>	<i>Camponotus punctulatus cruentatus</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Caenocholax fenyesei</i>	<i>Pheidole jelskii</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Caenocholax fenyesei</i>	<i>Pheidole radoszkowskii</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Caenocholax fenyesei</i>	<i>Camponotus atriaps</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Caenocholax fenyesei</i>	<i>Camponotus planatus</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Caenocholax fenyesei</i>	<i>Pheidole</i> sp.	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Caenocholax fenyesei</i>	<i>Myrmelachista zeledoni</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Caenocholax fenyesei</i>	<i>Crematogaster laeviuscula</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Caenocholax fenyesei</i>	<i>Solenopsis wagneri</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Caenocholax fenyesei texensis</i>	<i>Solenopsis invicta</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Caenocholax fenyesei waloffi</i>	<i>Dolichoderus bispinosus</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Myrmecolax borgmeieri</i>	<i>Eciton dulcius</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Myrmecolax incautus</i>	<i>Pachycondyla verena</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Myrmecolax incautus</i>	<i>Pachycondyla apicalis</i>	A	Ind.	Dir.	Ex

Continuation of Table A.1

Group	Parasite family	Parasite species	Ant species	Relationship ^a	Encounter mode ^b	Transmission mode ^c	Transmission location ^d
Strepsiptera	Myrmecolacidae	<i>Myrmecolax nietneri</i>	<i>Camponotus maculatus</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Myrmecolax ogloblini</i>	<i>Camponotus punctulatus</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Myrmecolax sp.</i>	<i>Camponotus sp.</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Stichotrema dallatorreanus</i>	<i>Camponotus papua</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Stichotrema robertsoni</i>	<i>Pheidole sp.</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Stichotrema vilhenai</i>	<i>Crematogaster sp.</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Stichotrema wigodzinsky</i>	<i>Camponotus spp.</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Stichotrema wigodzinsky</i>	<i>Pseudomyrmex sp.</i>	A	Ind.	Dir.	Ex
Strepsiptera	Myrmecolacidae	<i>Stichotrema wigodzinsky</i>	<i>Solenopsis richteri</i>	A	Ind.	Dir.	Ex

End of Table A.1

^a Relationship. A = Parasite, B = Parasitoid

^b Encounter mode. 1 = Primary, 2 = Secondary, Ind. = Independent, Mult. = Multiple, Unk. = Unknown

^c Transmission mode. Dir. = Direct, Indir. = Indirect

^d Transmission location. In = *In-nido*, Ex = *Ex-nido*

A.2 Ant associate records

Table A.2: Database of associates of ants

Associates of ants				
Group	Associate family	Associate species	Ant species	Relationship
Bacteria	Acidobacteriaceae	<i>Acidobacterium sp.</i>	<i>Solenopsis geminata</i>	Associate
	Acidobacteriaceae	<i>Acidobacterium sp.</i>	<i>Solenopsis invicta</i>	Associate
	Alcaligenaceae	<i>Achromobacter xylosoxidans 1</i>	<i>Solenopsis invicta</i>	Associate
	Alcaligenaceae	<i>Achromobacter xylosoxidans 2</i>	<i>Solenopsis invicta</i>	Associate
	Alcaligenaceae	<i>Alcaligenes faecalis</i>	<i>Solenopsis invicta</i>	Associate
	Anaeroplasmataceae	<i>Anaeroplasma sp.</i>	<i>Solenopsis invicta</i>	Associate
	Bacillaceae	<i>Bacillus cereus 2</i>	<i>Solenopsis invicta</i>	Associate
	Bacillaceae	<i>Bacillus cereus 3</i>	<i>Solenopsis invicta</i>	Associate
	Bacillaceae	<i>Bacillus pseudomycooides</i>	<i>Solenopsis invicta</i>	Associate
	Bacillaceae	<i>Bacillus sp.</i>	<i>Solenopsis geminata</i>	Associate
	Bacillaceae	<i>Bacillus sp.</i>	<i>Solenopsis invicta</i>	Associate
	Bacillaceae	<i>Bacillus sp. 2</i>	<i>Solenopsis invicta</i>	Associate
	Bacillaceae	<i>Bacillus sp. 5</i>	<i>Solenopsis invicta</i>	Associate
	Bacillaceae	<i>Bacillus sp. 6</i>	<i>Solenopsis invicta</i>	Associate
	Bacillaceae	<i>Bacillus sp. 7</i>	<i>Solenopsis invicta</i>	Associate
	Bacillaceae	<i>Bacillus sp. 8</i>	<i>Solenopsis invicta</i>	Associate
	Bacillaceae	<i>Bacillus thuringiensis</i>	<i>Solenopsis invicta</i>	Associate
	Bacillaceae	<i>Geobacillus sp.</i>	<i>Solenopsis invicta</i>	Associate
	Bacillaceae	<i>Lysinibacillus fusiformis 1</i>	<i>Solenopsis invicta</i>	Associate
	Bacteroidaceae	<i>Bacteroides sp.</i>	<i>Solenopsis geminata</i>	Associate
Bacteroidaceae	<i>Bacteroides sp.</i>	<i>Solenopsis invicta</i>	Associate	
Bradyrhizobiaceae	<i>Bradyrhizobium sp.</i>	<i>Solenopsis geminata</i>	Associate	

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Bradyrhizobiaceae	<i>Bradyrhizobium sp.</i>	<i>Solenopsis invicta</i>	Associate
	Brevibacteriaceae	<i>Brevibacterium frigoritolerans</i>	<i>Solenopsis invicta</i>	Associate
	Burkholderiaceae	<i>Pandoraea sp. 1</i>	<i>Solenopsis invicta</i>	Associate
	Burkholderiaceae	<i>Pandoraea sp. 2</i>	<i>Solenopsis invicta</i>	Associate
	Burkholderiaceae	<i>Pandoraea sp. 3</i>	<i>Solenopsis invicta</i>	Associate
	Caldilineaceae	<i>Caldilinea sp.</i>	<i>Solenopsis invicta</i>	Associate
	Caulobacteraceae	<i>Brevundimonas diminuta</i>	<i>Solenopsis invicta</i>	Associate
	Caulobacteraceae	<i>Brevundimonas sp.</i>	<i>Solenopsis invicta</i>	Associate
	Clostridiaceae	<i>Clostridium sp.</i>	<i>Solenopsis geminata</i>	Associate
	Clostridiaceae	<i>Clostridium sp.</i>	<i>Solenopsis invicta</i>	Associate
	Comamonadaceae	<i>Acidovorax sp.</i>	<i>Solenopsis geminata</i>	Associate
	Comamonadaceae	<i>Comamonas sp.</i>	<i>Solenopsis geminata</i>	Associate
	Comamonadaceae	<i>Comamonas sp.</i>	<i>Solenopsis invicta</i>	Associate
	Comamonadaceae	<i>Schlegelella sp.</i>	<i>Solenopsis invicta</i>	Associate
	Conexibacteraceae	<i>Conexibacter sp.</i>	<i>Solenopsis geminata</i>	Associate
	Conexibacteraceae	<i>Conexibacter sp.</i>	<i>Solenopsis invicta</i>	Associate
	Corynebacteriaceae	<i>Corynebacterium sp.</i>	<i>Solenopsis geminata</i>	Associate
	Cystobacteraceae	<i>Cystobacter sp.</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Enterobacter amnigenus</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Enterobacter sp. 1</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Erwinia sp.</i>	<i>Solenopsis geminata</i>	Associate
	Enterobacteriaceae	<i>Erwinia sp.</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Klebsiella oxytoca</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Moellerella sp.</i>	<i>Solenopsis geminata</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Enterobacteriaceae	<i>Morganella sp.</i>	<i>Solenopsis geminata</i>	Associate
	Enterobacteriaceae	<i>Pantoea sp.</i>	<i>Solenopsis geminata</i>	Associate
	Enterobacteriaceae	<i>Pantoea sp.</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Rahnella sp.</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Serratia liquefaciens</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Serratia marcescens 2</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Serratia marcescens 3</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Serratia sp. 1</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Serratia sp. 2</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Serratia sp. 3</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Serratia sp. 4</i>	<i>Solenopsis invicta</i>	Associate
	Enterobacteriaceae	<i>Serratia symbiotica</i>	<i>Formica cinerea</i>	Associate
	Enterococcaceae	<i>Enterococcus sp.</i>	<i>Solenopsis geminata</i>	Associate
	Enterococcaceae	<i>Enterococcus sp.</i>	<i>Solenopsis invicta</i>	Associate
	Enterococcaceae	<i>Vagococcus sp.</i>	<i>Solenopsis geminata</i>	Associate
	Folliculinidae	<i>Folliculinopsis sp.</i>	<i>Solenopsis invicta</i>	Associate
	Frankiaceae	<i>Frankia sp.</i>	<i>Solenopsis geminata</i>	Associate
	Gemmatimonadaceae	<i>Gemmatimonas sp.</i>	<i>Solenopsis geminata</i>	Associate
	Gemmatimonadaceae	<i>Gemmatimonas sp.</i>	<i>Solenopsis invicta</i>	Associate
	Geobacteraceae	<i>Geopsychrobacter sp.</i>	<i>Solenopsis invicta</i>	Associate
	Geobacteraceae	<i>Geothermobacter sp.</i>	<i>Solenopsis invicta</i>	Associate
	Helicobacteraceae	<i>Sulfurimonas sp.</i>	<i>Solenopsis invicta</i>	Associate
	IncertaeSedis	<i>Exiguobacterium sp.</i>	<i>Solenopsis geminata</i>	Associate
	IncertaeSedis	<i>Methylibium sp.</i>	<i>Solenopsis geminata</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Intrasporangiaceae	<i>Terrabacter sp.</i>	<i>Solenopsis geminata</i>	Associate
	Lactobacillaceae	<i>Lactobacillus sp.</i>	<i>Solenopsis invicta</i>	Associate
	Methylobacteriaceae	<i>Methylobacterium sp.</i>	<i>Solenopsis geminata</i>	Associate
	Methylocystaceae	<i>Methylocystis sp.</i>	<i>Solenopsis geminata</i>	Associate
	Methylocystaceae	<i>Methylocystis sp.</i>	<i>Solenopsis invicta</i>	Associate
	Microbacteriaceae	<i>Agromyces sp.</i>	<i>Solenopsis geminata</i>	Associate
	Microbacteriaceae	<i>Agromyces sp.</i>	<i>Solenopsis invicta</i>	Associate
	Microbacteriaceae	<i>Curtobacterium sp.</i>	<i>Solenopsis invicta</i>	Associate
	Micrococcaceae	<i>Arthrobacter sp.</i>	<i>Solenopsis geminata</i>	Associate
	Micrococcaceae	<i>Arthrobacter sp.</i>	<i>Solenopsis invicta</i>	Associate
	Moraxellaceae	<i>Acinetobacter guillouiae</i>	<i>Solenopsis invicta</i>	Associate
	Moraxellaceae	<i>Acinetobacter sp.</i>	<i>Solenopsis geminata</i>	Associate
	Moraxellaceae	<i>Acinetobacter sp.</i>	<i>Solenopsis invicta</i>	Associate
	Mycobacteriaceae	<i>Mycobacterium sp.</i>	<i>Solenopsis geminata</i>	Associate
	Mycobacteriaceae	<i>Mycobacterium sp.</i>	<i>Solenopsis invicta</i>	Associate
	Nocardioideaceae	<i>Aeromicrobium sp.</i>	<i>Solenopsis geminata</i>	Associate
	Nocardioideaceae	<i>Aeromicrobium sp.</i>	<i>Solenopsis invicta</i>	Associate
	Nocardioideaceae	<i>Marmoricola sp.</i>	<i>Solenopsis geminata</i>	Associate
	Nocardioideaceae	<i>Marmoricola sp.</i>	<i>Solenopsis invicta</i>	Associate
	Nocardioideaceae	<i>Nocardioides sp.</i>	<i>Solenopsis geminata</i>	Associate
	Nocardioideaceae	<i>Nocardioides sp.</i>	<i>Solenopsis invicta</i>	Associate
	Oxalobacteraceae	<i>Duganella sp.</i>	<i>Solenopsis geminata</i>	Associate
	Oxalobacteraceae	<i>Herbaspirillum sp.</i>	<i>Solenopsis invicta</i>	Associate
	Oxalobacteraceae	<i>Janthinobacterium sp.</i>	<i>Solenopsis geminata</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Oxalobacteraceae	<i>Janthinobacterium sp.</i>	<i>Solenopsis invicta</i>	Associate
	Paenibacillaceae	<i>Brevibacillus laterosporus</i>	<i>Solenopsis invicta</i>	Associate
	Paenibacillaceae	<i>Paenibacillus lautus</i>	<i>Solenopsis invicta</i>	Associate
	Paenibacillaceae	<i>Paenibacillus macerans</i>	<i>Solenopsis invicta</i>	Associate
	Paenibacillaceae	<i>Paenibacillus sp.</i>	<i>Solenopsis invicta</i>	Associate
	Paenibacillaceae	<i>Paenibacillus sp.</i>	<i>Solenopsis geminata</i>	Associate
	Paenibacillaceae	<i>Paenibacillus sp.</i>	<i>Solenopsis invicta</i>	Associate
	Paenibacillaceae	<i>Paenibacillus sp. 1</i>	<i>Solenopsis invicta</i>	Associate
	Paenibacillaceae	<i>Paenibacillus sp. 2</i>	<i>Solenopsis invicta</i>	Associate
	Patulibacteraceae	<i>Patulibacter sp.</i>	<i>Solenopsis geminata</i>	Associate
	Patulibacteraceae	<i>Patulibacter sp.</i>	<i>Solenopsis invicta</i>	Associate
	Phyllobacteriaceae	<i>Mesorhizobium sp.</i>	<i>Solenopsis geminata</i>	Associate
	Propionibacteriaceae	<i>Propionibacterium sp.</i>	<i>Solenopsis geminata</i>	Associate
	Propionibacteriaceae	<i>Propionibacterium sp.</i>	<i>Solenopsis invicta</i>	Associate
	Pseudomonadaceae	<i>Pseudomonas protegens</i>	<i>Solenopsis invicta</i>	Associate
	Pseudomonadaceae	<i>Pseudomonas putida</i>	<i>Solenopsis invicta</i>	Associate
	Pseudomonadaceae	<i>Pseudomonas sp.</i>	<i>Solenopsis geminata</i>	Associate
	Pseudomonadaceae	<i>Pseudomonas sp.</i>	<i>Solenopsis invicta</i>	Associate
	Pseudomonadaceae	<i>Pseudomonas sp. 1</i>	<i>Solenopsis invicta</i>	Associate
	Pseudomonadaceae	<i>Pseudomonas sp. 2</i>	<i>Solenopsis invicta</i>	Associate
	Pseudonocardiaceae	<i>Actinomycetospora sp.</i>	<i>Solenopsis geminata</i>	Associate
	Pseudonocardiaceae	<i>Actinomycetospora sp.</i>	<i>Solenopsis invicta</i>	Associate
	Pseudonocardiaceae	<i>Pseudonocardia sp.</i>	<i>Solenopsis geminata</i>	Associate
	Pseudonocardiaceae	<i>Pseudonocardia sp.</i>	<i>Solenopsis invicta</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Rhodobacteraceae	<i>Loktanella sp.</i>	<i>Solenopsis invicta</i>	Associate
	Rhodobacteraceae	<i>Thalassobacter sp.</i>	<i>Solenopsis invicta</i>	Associate
	Rhodocyclaceae	<i>Zoogloea sp.</i>	<i>Solenopsis geminata</i>	Associate
	Rhodocyclaceae	<i>Zoogloea sp.</i>	<i>Solenopsis invicta</i>	Associate
	Solirubrobacteraceae	<i>Solirubrobacter sp.</i>	<i>Solenopsis geminata</i>	Associate
	Solirubrobacteraceae	<i>Solirubrobacter sp.</i>	<i>Solenopsis invicta</i>	Associate
	Sphingomonadaceae	<i>Sphingomonas sp.</i>	<i>Solenopsis geminata</i>	Associate
	Sphingomonadaceae	<i>Sphingomonas sp.</i>	<i>Solenopsis invicta</i>	Associate
	Spiroplasmataceae	<i>Spiroplasma sp.</i>	<i>Solenopsis geminata</i>	Associate
	Staphylococcaceae	<i>Jeotgalicoccus halotolerans</i>	<i>Solenopsis invicta</i>	Associate
	Staphylococcaceae	<i>Staphylococcus epidermidis</i>	<i>Solenopsis invicta</i>	Associate
	Staphylococcaceae	<i>Staphylococcus sp.</i>	<i>Solenopsis geminata</i>	Associate
	Staphylococcaceae	<i>Staphylococcus sp.</i>	<i>Solenopsis invicta</i>	Associate
	Streptococcaceae	<i>Lactococcus sp.</i>	<i>Solenopsis geminata</i>	Associate
	Streptococcaceae	<i>Lactococcus sp.</i>	<i>Solenopsis invicta</i>	Associate
	Streptococcaceae	<i>Streptococcus sp.</i>	<i>Solenopsis geminata</i>	Associate
	Streptococcaceae	<i>Streptococcus sp.</i>	<i>Solenopsis invicta</i>	Associate
	Streptomycetaceae	<i>Streptomyces sp.</i>	<i>Solenopsis geminata</i>	Associate
	Streptomycetaceae	<i>Streptomyces sp.</i>	<i>Solenopsis invicta</i>	Associate
	Xanthomonadaceae	<i>Stenotrophomonas maltophilia</i>	<i>Solenopsis invicta</i>	Associate
	Xanthomonadaceae	<i>Stenotrophomonas sp.</i>	<i>Solenopsis geminata</i>	Associate
	Xanthomonadaceae	<i>Stenotrophomonas sp.</i>	<i>Solenopsis invicta</i>	Associate
Fungi	Cordycipitaceae	<i>Corydceps amoene-roseus</i>	<i>Cataulacus guineensis</i>	Associate
	Cordycipitaceae	<i>Corydceps amoene-roseus</i>	<i>Crematogaster sp.</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Cordycipitaceae	<i>Corydiceps amoene-roseus</i>	<i>Crematogaster striatula</i>	Associate
	Cordycipitaceae	<i>Corydiceps amoene-roseus</i>	<i>Phrynonoponera gabonensis</i>	Associate
	Cordycipitaceae	<i>Gibellula carnata</i>	<i>Paltothyreus tarsatus</i>	Associate
	Cordycipitaceae	<i>Gibellula formicarium</i>	<i>Camponotus sp.</i>	Associate
	Cordycipitaceae	<i>Gibellula formicarium</i>	<i>Phasmomyrmex paradoxa</i>	Associate
	Cordycipitaceae	<i>Gibellula liberiana</i>	<i>Pachycondyla tarsata</i>	Associate
	Cordycipitaceae	<i>Gibellula liberiana</i>	<i>Paltothyreus tarsatus</i>	Associate
	Cordycipitaceae	<i>Pseudogibellula formicarum</i>	<i>Crematogaster bequaerti</i>	Hyperparasite
	Cordycipitaceae	<i>Pseudogibellula formicarum</i>	<i>Crematogaster clariventris</i>	Hyperparasite
	Cordycipitaceae	<i>Pseudogibellula formicarum</i>	<i>Crematogaster striatula</i>	Hyperparasite
	Cordycipitaceae	<i>Pseudogibellula formicarum</i>	<i>Macromischoides aculeatus</i>	Hyperparasite
	Cordycipitaceae	<i>Pseudogibellula formicarum</i>	<i>Macromischoides inermis</i>	Hyperparasite
	Cordycipitaceae	<i>Pseudogibellula formicarum</i>	<i>Paltothyreus tarsatus</i>	Hyperparasite
	Cunninghamellaceae	<i>Absidia corymbifera</i>	<i>Paratrechina longicornis</i>	Associate
	Cunninghamellaceae	<i>Cunninghamella equinalata</i>	<i>Paratrechina longicornis</i>	Associate
	Cunninghamellaceae	<i>Cunninghamella polymorpha</i>	<i>Paratrechina longicornis</i>	Associate
	Davidiellaceae	<i>Cladosporium sp.</i>	<i>Paratrechina longicornis</i>	Associate
	Endomycetaceae	<i>Geotrichum sp.</i>	<i>Paratrechina longicornis</i>	Associate
	Hypocreaceae	<i>Acremonium sp.</i>	<i>Paratrechina longicornis</i>	Associate
	Hypocreaceae	<i>Acremonium strictum</i>	<i>Solenopsis richteri</i>	Associate
	Hypocreaceae	<i>Hypocrea lixii</i>	<i>Solenopsis invicta</i>	Associate
	Hypocreaceae	<i>Trichoderma atroviride</i>	<i>Atta sp.</i>	Associate
	IncertaeSedis	<i>Myrmecomycetes annellisae</i>	<i>Solenopsis sp.</i>	Associate
	Nectriaceae	<i>Fusarium equiseti</i>	<i>Solenopsis invicta</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Nectriaceae	<i>Fusarium graminearum</i>	<i>Atta sp.</i>	Associate
	Nectriaceae	<i>Fusarium oxysporum</i>	<i>Atta sp.</i>	Associate
	Nectriaceae	<i>Fusarium oxysporum</i>	<i>Solenopsis invicta</i>	Associate
	Nectriaceae	<i>Fusarium solani</i>	<i>Atta sp.</i>	Associate
	Ophiocordycipitaceae	<i>Purpureocillium lilacinum</i>	<i>Atta sp.</i>	Associate
	Ophiocordycipitaceae	<i>Purpureocillium lilacinum</i>	<i>Paratrechina longicornis</i>	Associate
	Ophiocordycipitaceae	<i>Purpureocillium lilacinum</i>	<i>Myrmecia nigriscapa</i>	Associate
	Ophiocordycipitaceae	<i>Purpureocillium lilacinum</i>	<i>Solenopsis richteri</i>	Associate
	Ophiocordycipitaceae	<i>Purpureocillium lilacinum</i>	<i>Formica selysi</i>	Associate
	Ophiostomataceae	<i>Sporothrix insectorum</i>	<i>Crematogaster bequaerti</i>	Hyperparasite
	Ophiostomataceae	<i>Sporothrix insectorum</i>	<i>Macromischoides inermis</i>	Hyperparasite
	Ophiostomataceae	<i>Sporothrix insectorum</i>	<i>Paltothyreus tarsatus</i>	Hyperparasite
	Plectosphaerellaceae	<i>Verticillium nodulosum</i>	<i>Dorylus sp.</i>	Associate
	Plectosphaerellaceae	<i>Verticillium nodulosum</i>	<i>Macromischoides inermis</i>	Associate
	Plectosphaerellaceae	<i>Verticillium nodulosum</i>	<i>Paltothyreus tarsatus</i>	Associate
	Pleosporaceae	<i>Cochiobolus kusanoi</i>	<i>Solenopsis invicta</i>	Associate
	Pleosporaceae	<i>Curvularia sp.</i>	<i>Solenopsis invicta</i>	Associate
	Trichocomaceae	<i>Aspergillus candidus</i>	<i>Paratrechina longicornis</i>	Associate
	Trichocomaceae	<i>Aspergillus flavipes</i>	<i>Solenopsis invicta</i>	Associate
	Trichocomaceae	<i>Aspergillus nomius</i>	<i>Solenopsis invicta</i>	Associate
	Trichocomaceae	<i>Aspergillus ochraceus</i>	<i>Atta bisphaerica</i>	Associate
	Trichocomaceae	<i>Aspergillus ochraceus</i>	<i>Paratrechina longicornis</i>	Associate
	Trichocomaceae	<i>Aspergillus parasiticus</i>	<i>Formica selysi</i>	Associate
	Trichocomaceae	<i>Aspergillus tubingensis</i>	<i>Solenopsis invicta</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Trichocomaceae	<i>Aspergillus versicolor</i>	<i>Paratrechina longicornis</i>	Associate
	Trichocomaceae	<i>Neosartorya fischeri</i>	<i>Solenopsis invicta</i>	Associate
	Trichocomaceae	<i>Penicillium sizovae</i>	<i>Formica selysi</i>	Associate
	Trichocomaceae	<i>Penicillium skrjabinii</i>	<i>Formica selysi</i>	Associate
	Trichocomaceae	<i>Penicillium sp.</i>	<i>Paratrechina longicornis</i>	Associate
	Trichocomaceae	<i>Penicillium spinulosum</i>	<i>Solenopsis invicta</i>	Associate
	Trichocomaceae	<i>Petromyces alliaceus</i>	<i>Formica selysi</i>	Associate
Hymenoptera	Bethylidae	<i>Pseudisobrachium sp.</i>	<i>Solenopsis saevissima</i>	Associate
	Bethylidae	<i>Pseudisobrachium terresi</i>	<i>Aphaenogaster relict</i>	Associate
	Braconidae	<i>Paralypsis enervis</i>	<i>Lasius niger</i>	Associate
	Diapriidae	<i>Asolenopsis rufa</i>	<i>Neivamyrmex carettei</i>	Associate
	Diapriidae	<i>Basalys sp.</i>	<i>Linepithema humile</i>	Associate
	Diapriidae	<i>Labridopria sp.</i>	<i>Labidus sp.</i>	Associate
	Diapriidae	<i>Mimopria barbata</i>	<i>Nomamyrmex esenbecki</i>	Associate
	Diapriidae	<i>Mimopria campbellorum</i>	<i>Eciton hamatum</i>	Associate
	Diapriidae	<i>Mimopria comes</i>	<i>Eciton schlechtendali</i>	Associate
	Diapriidae	<i>Mimopria comes</i>	<i>Labidus coecus</i>	Associate
	Diapriidae	<i>Mimopria comes</i>	<i>Nomamyrmex esenbecki</i>	Associate
	Diapriidae	<i>Mimopria ecitophila</i>	<i>Eciton hamatum</i>	Associate
	Diapriidae	<i>Myrmecopria mellea</i>	<i>Nomamyrmex sp.</i>	Associate
	Diapriidae	<i>Notoxoides pedissequus</i>	<i>Neivamyrmex pseudops</i>	Associate
	Diapriidae	<i>Notoxoides pronotalis</i>	<i>Eciton dulcium</i>	Associate
	Diapriidae	<i>Notoxoides pronotalis</i>	<i>Neivamyrmex sulcatus</i>	Associate
	Diapriidae	<i>Pentapria nodicornis</i>	<i>Solenopsis saevissima</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Diapriidae	<i>Solenopsis imitatrix</i>	<i>Solenopsis fugax</i>	Associate
	Diapriidae	<i>Spilomicrus sp.</i>	<i>Solenopsis sp.</i>	Associate
	Encyrtidae	<i>Aenasius tachigaliae</i>	<i>Azteca xanthochroa</i>	Associate
	Encyrtidae	<i>Aenasius tachigaliae</i>	<i>Crematogaster curvispinosa</i>	Associate
	Encyrtidae	<i>Aenasius tachigaliae</i>	<i>Crematogaster sp.</i>	Associate
	Encyrtidae	<i>Anagyrus lopezi</i>	<i>Camponotus acvapimensis</i>	Associate
	Encyrtidae	<i>Anagyrus lopezi</i>	<i>Camponotus flavomarginatus</i>	Associate
	Encyrtidae	<i>Anagyrus lopezi</i>	<i>Lepisiota capensis</i>	Associate
	Encyrtidae	<i>Anagyrus lopezi</i>	<i>Monomorium sp.</i>	Associate
	Encyrtidae	<i>Anagyrus lopezi</i>	<i>Oecophylla smaragdina</i>	Associate
	Encyrtidae	<i>Anagyrus saccharicola</i>	<i>Pheidole megacephala</i>	Associate
	Encyrtidae	<i>Ananusia longiscapus</i>	<i>Iridomyrmex domestica</i>	Associate
	Encyrtidae	<i>Anicetus beneficus</i>	<i>Lasius niger</i>	Associate
	Encyrtidae	<i>Arketypon vaderi</i>	<i>Camponotus sp.</i>	Associate
	Encyrtidae	<i>Astymachus phainae</i>	<i>Crematogaster sp.</i>	Associate
	Encyrtidae	<i>Bothriothorax intermedius</i>	<i>Lasius niger</i>	Associate
	Encyrtidae	<i>Comperiella bifasciata</i>	<i>Formica aerella</i>	Associate
	Encyrtidae	<i>Comperiella bifasciata</i>	<i>Iridomyrmex humilis</i>	Associate
	Encyrtidae	<i>Comperiella bifasciata</i>	<i>Linepithema humile</i>	Associate
	Encyrtidae	<i>Comperiella bifasciata</i>	<i>Solenopsis xyloni</i>	Associate
	Encyrtidae	<i>Encyrtus ingae</i>	<i>Crematogaster dohrni</i>	Associate
	Encyrtidae	<i>Encyrtus ingae</i>	<i>Crematogaster sp.</i>	Associate
	Encyrtidae	<i>Encyrtus ludmilae</i>	<i>Crematogaster sp.</i>	Associate
	Encyrtidae	<i>Holcencyrtus wheeleri</i>	<i>Pheidole sp.</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Encyrtidae	<i>Holcencyrtus wheeleri</i>	<i>Pheidole tepicana</i>	Associate
	Encyrtidae	<i>Holcencyrtus wheeleri</i>	<i>Pheidole wheeleri</i>	Associate
	Encyrtidae	<i>Leptomastix dactylopii</i>	<i>Camponotus nylanderi</i>	Associate
	Encyrtidae	<i>Leptomastix dactylopii</i>	<i>Linepithema humile</i>	Associate
	Encyrtidae	<i>Leptomastix dactylopii</i>	<i>Tapinoma erraticum</i>	Associate
	Encyrtidae	<i>Metaphycus annekei</i>	<i>Linepithema humile</i>	Associate
	Encyrtidae	<i>Metaphycus hageni</i>	<i>Linepithema humile</i>	Associate
	Encyrtidae	<i>Metaphycus lounsburyi</i>	<i>Linepithema humile</i>	Associate
	Encyrtidae	<i>Metaphycus monastyrskii</i>	<i>Crematogaster sp.</i>	Associate
	Encyrtidae	<i>Microterys roseni</i>	<i>Dolichoderus bituberculatus</i>	Associate
	Encyrtidae	<i>Microterys roseni</i>	<i>Dolichoderus sp.</i>	Associate
	Encyrtidae	<i>Ooencyrtus sp.</i>	<i>Camponotus brutus</i>	Associate
	Encyrtidae	<i>Ooencyrtus sp.</i>	<i>Myrmicaria opaciventris</i>	Associate
	Encyrtidae	<i>Paraphaenodiscus udayveeri</i>	<i>Oecophylla smaragdina</i>	Associate
	Encyrtidae	<i>Pheidoloxenus wheeleri</i>	<i>Pheidole ceres</i>	Associate
	Encyrtidae	<i>Pheidoloxenus wheeleri</i>	<i>Pheidole instabilis</i>	Associate
	Encyrtidae	<i>Syrphophagus aphidivorus</i>	<i>Lasius niger</i>	Associate
	Encyrtidae	<i>Syrphophagus aphidivorus</i>	<i>Myrmica laevinodis</i>	Associate
	Eulophidae	<i>Achrysocharoides niveipes</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Chrysocharis assis</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Chrysocharis collaris</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Chrysocharis nephereus</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Chrysocharis orbicularis</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Chrysocharis pilicoxa</i>	<i>Formica aquilona</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Eulophidae	<i>Cirrospilus curvineurus</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Cirrospilus vittatus</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Derostenus gemmeus</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Di cladocerus westwoodii</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Elachterus artaeus</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Horismenus microdonophagus</i>	<i>Camponotus sp.</i>	Associate
	Eulophidae	<i>Horismenus sp.</i>	<i>Eciton burchelli</i>	Associate
	Eulophidae	<i>Microdonophagus woodleyi</i>	<i>Technomyrmex fulvus</i>	Associate
	Eulophidae	<i>Myrmobomyia malayana</i>	<i>Dolichoderus sp.</i>	Associate
	Eulophidae	<i>Pediobius acraconae</i>	<i>Camponotus africana</i>	Associate
	Eulophidae	<i>Pediobius acraconae</i>	<i>Crematogaster depressa</i>	Associate
	Eulophidae	<i>Pediobius metallicus</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Pnigalio longulus</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Pnigalio pectinicornis</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Sympiesis gordius</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Sympiesis sericeicornis</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Sympiesis xanthostoma</i>	<i>Formica aquilona</i>	Associate
	Eulophidae	<i>Tetrastichus sp.</i>	<i>Myrmecocystus mexicanus</i>	Associate
	Eurytomidae	<i>Camponotophilus delvarei</i>	<i>Camponotus textor</i>	Associate
	Eurytomidae	<i>Sycophila sp.</i>	<i>Formica obscuripes</i>	Associate
	Ichneumonidae	<i>Pseomachus sp.</i>	<i>Formica sp.</i>	Associate
	Ichneumonidae	<i>Pseomachus sp.</i>	<i>Myrmica sp.</i>	Associate
Diptera	Phoridae	<i>Acontistoptera brasiliensis</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Acontistoptera melanderi</i>	<i>Neivamyrmex pilosus</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Phoridae	<i>Acontistoptera melanderi</i>	<i>Neivamyrmex opacithorax</i>	Associate
	Phoridae	<i>Adelopteromyia parvipennis</i>	<i>Eciton burchelli</i>	Associate
	Phoridae	<i>Adelopteromyia parvipennis</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Adelopteromyia propinqua</i>	<i>Eciton burchelli</i>	Associate
	Phoridae	<i>Adelopteromyia propinqua</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Aenictacantha crassitarsalis</i>	<i>Aenictus decolor</i>	Associate
	Phoridae	<i>Aenictacantha sentifera</i>	<i>Aenictus aratus</i>	Associate
	Phoridae	<i>Aenictacantha sentifera</i>	<i>Aenictus sp.</i>	Associate
	Phoridae	<i>Aenigmatopoeus cucullatus</i>	<i>Dorylus fulvus</i>	Associate
	Phoridae	<i>Aenigmatopoeus cucullatus</i>	<i>Dorylus sp.</i>	Associate
	Phoridae	<i>Aenigmatopoeus kohli</i>	<i>Dorylus brevipennis</i>	Associate
	Phoridae	<i>Aenigmatopoeus kohli</i>	<i>Dorylus emeyi</i>	Associate
	Phoridae	<i>Aenigmatopoeus kohli</i>	<i>Dorylus kohli</i>	Associate
	Phoridae	<i>Aenigmatopoeus orbicularis</i>	<i>Dorylus nigricans sub. molestus</i>	Associate
	Phoridae	<i>Aenigmatopoeus orbicularis</i>	<i>Dorylus nigricans sub. sjoestdti</i>	Associate
	Phoridae	<i>Aenigmatopoeus pseudokohli</i>	<i>Dorylus wilverthi</i>	Associate
	Phoridae	<i>Aenigmatopoeus sequax</i>	<i>Dorylus nigricans sub. molestus</i>	Associate
	Phoridae	<i>Aenigmatopoeus sequax</i>	<i>Aenictus eugenii</i>	Associate
	Phoridae	<i>Aenigmatopoeus sodalis</i>	<i>Aenictus sp.</i>	Associate
	Phoridae	<i>Aenigmatopoeus sodalis</i>	<i>Dorylus braunsi</i>	Associate
	Phoridae	<i>Aenigmatopoeus sodalis</i>	<i>Dorylus brevipennis</i>	Associate
	Phoridae	<i>Apterophora attophila</i>	<i>Atta sexdens</i>	Associate
	Phoridae	<i>Apterophora attophila</i>	<i>Eciton hamatum</i>	Associate
	Phoridae	<i>Apterophora attophila</i>	<i>Eciton burchelli</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Phoridae	<i>Apterophora attophila</i>	<i>Solenopsis geminata</i>	Associate
	Phoridae	<i>Apterophora borgmeieri</i>	<i>Atta sexdens</i>	Associate
	Phoridae	<i>Apterophora bragancai</i>	<i>Atta sexdens</i>	Associate
	Phoridae	<i>Apterophora caliginosa</i>	<i>Eciton hamatum</i>	Associate
	Phoridae	<i>Cataclinusa bucki</i>	<i>Neoponera crenata</i>	Associate
	Phoridae	<i>Cataclinusa pachycondylae</i>	<i>Pachycondyla harpax</i>	Kleptoparasite
	Phoridae	<i>Chonocephalus buccatus</i>	<i>Eciton burchelli</i>	Associate
	Phoridae	<i>Diploneura brincki</i>	<i>Dorylus braunsi</i>	Associate
	Phoridae	<i>Dohrniphora apharea</i>	<i>Odontomachus mormo</i>	Predator
	Phoridae	<i>Dohrniphora cornuta</i>	<i>Eciton burchelli</i>	Predator
	Phoridae	<i>Dohrniphora curvispinosa</i>	<i>Atta bidens</i>	Predator
	Phoridae	<i>Dohrniphora diminuens</i>	<i>Dorylus sp.</i>	Predator
	Phoridae	<i>Dohrniphora ecitophila</i>	<i>Eciton burchelli</i>	Predator
	Phoridae	<i>Dohrniphora ecitophila</i>	<i>Eciton dulcius crassinode</i>	Predator
	Phoridae	<i>Dohrniphora ecitophila</i>	<i>Eciton mexicanum</i>	Predator
	Phoridae	<i>Dohrniphora femoralis</i>	<i>Eciton burchelli</i>	Predator
	Phoridae	<i>Dohrniphora fuscicoxa</i>	<i>Atta sexdens</i>	Predator
	Phoridae	<i>Dohrniphora longirostrata</i>	<i>Odontomachus haematodus</i>	Predator
	Phoridae	<i>Dohrniphora longirostrata</i>	<i>Odontomachus sp.</i>	Predator
	Phoridae	<i>Dohrniphora oricilla</i>	<i>Pachycondyla obscuricornis</i>	Predator
	Phoridae	<i>Dohrniphora paraguayana</i>	<i>Atta sexdens</i>	Predator
	Phoridae	<i>Dohrniphora sp.</i>	<i>Eciton hamatum</i>	Predator
	Phoridae	<i>Dohrniphora sp.</i>	<i>Eciton burchelli</i>	Predator
	Phoridae	<i>Dohrniphora sp.</i>	<i>Ectatomma lugens</i>	Predator

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Phoridae	<i>Dohrniphora sp.</i>	<i>Odontomachus chelififer</i>	Predator
	Phoridae	<i>Dohrniphora sp.</i>	<i>Odontomachus haematodus</i>	Predator
	Phoridae	<i>Dohrniphora sp.</i>	<i>Odontomachus mormo</i>	Predator
	Phoridae	<i>Dohrniphora sp.</i>	<i>Pachycondyla unidentata</i>	Predator
	Phoridae	<i>Dohrniphora sp.</i>	<i>Pachycondyla villosa</i>	Predator
	Phoridae	<i>Dohrniphora sp. N</i>	<i>Aenictus cornutus</i>	Predator
	Phoridae	<i>Dohrniphora sp. N</i>	<i>Aenictus gracilis</i>	Predator
	Phoridae	<i>Ecitomyia juxtaposita</i>	<i>Neoponera laevigata</i>	Associate
	Phoridae	<i>Ecitomyia wheeleri</i>	<i>Neivamyrmex scopifer</i>	Associate
	Phoridae	<i>Ecitomyia wheeleri</i>	<i>Neivamyrmex sumichrasti</i>	Associate
	Phoridae	<i>Ecitomyia wheeleri</i>	<i>Labidus coecus</i>	Associate
	Phoridae	<i>Ecitomyia wheeleri</i>	<i>Neivamyrmex alfaroi</i>	Associate
	Phoridae	<i>Ecitomyia wheeleri</i>	<i>Neivamyrmex nigrescens</i>	Associate
	Phoridae	<i>Ecitomyia wheeleri</i>	<i>Eciton coecum</i>	Associate
	Phoridae	<i>Ecitomyia wheeleri</i>	<i>Eciton schmitti</i>	Associate
	Phoridae	<i>Ecitomyia wheeleri</i>	<i>Neivamyrmex pilosus</i>	Associate
	Phoridae	<i>Ecitophora breviptera</i>	<i>Nomamyrmex esenbecki</i>	Associate
	Phoridae	<i>Ecitophora breviptera</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Ecitophora breviptera</i>	<i>Eciton burchelli</i>	Associate
	Phoridae	<i>Ecitophora bruchi</i>	<i>Eciton mexicanum</i>	Associate
	Phoridae	<i>Ecitophora bruchi</i>	<i>Eciton burchelli</i>	Associate
	Phoridae	<i>Ecitophora bruchi</i>	<i>Eciton dulcius crassinode</i>	Associate
	Phoridae	<i>Ecitophora bruchi</i>	<i>Eciton vagans</i>	Associate
	Phoridae	<i>Ecitophora bruchi</i>	<i>Labidus coecus</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Phoridae	<i>Ecitophora bruchi</i>	<i>Nomamyrmex hartigii</i>	Associate
	Phoridae	<i>Ecitophora collegiana</i>	<i>Eciton burchellii</i>	Associate
	Phoridae	<i>Ecitophora collegiana</i>	<i>Eciton hamatum</i>	Associate
	Phoridae	<i>Ecitophora collegiana</i>	<i>Neivamyrmex sumichrasti</i>	Associate
	Phoridae	<i>Ecitophora collegiana</i>	<i>Eciton dulcius crassinode</i>	Associate
	Phoridae	<i>Ecitophora collegiana</i>	<i>Eciton mexicanum</i>	Associate
	Phoridae	<i>Ecitophora collegiana</i>	<i>Eciton vagans</i>	Associate
	Phoridae	<i>Ecitophora comes</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Ecitophora comes</i>	<i>Neivamyrmex sumichrasti</i>	Associate
	Phoridae	<i>Ecitophora comes</i>	<i>Eciton lucanoides</i>	Associate
	Phoridae	<i>Ecitophora costaricensis</i>	<i>Neivamyrmex impudens</i>	Associate
	Phoridae	<i>Ecitophora costaricensis</i>	<i>Eciton lucanoides</i>	Associate
	Phoridae	<i>Ecitophora costaricensis</i>	<i>Labidus coecus</i>	Associate
	Phoridae	<i>Ecitophora fidelis</i>	<i>Labidus coecus</i>	Associate
	Phoridae	<i>Ecitophora fidelis</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Ecitophora parva</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Ecitophora parva</i>	<i>Eciton dulcium</i>	Associate
	Phoridae	<i>Ecitophora parva</i>	<i>Neivamyrmex pilosus</i>	Associate
	Phoridae	<i>Ecitophora pilosula</i>	<i>Eciton dulcius crassinode</i>	Associate
	Phoridae	<i>Ecitophora pilosula</i>	<i>Eciton mexicanum</i>	Associate
	Phoridae	<i>Ecitophora sp.</i>	<i>Eciton burchelli</i>	Associate
	Phoridae	<i>Ecitophora sp.</i>	<i>Eciton hamatum</i>	Associate
	Phoridae	<i>Ecitophora sp.</i>	<i>Eciton mexicanum</i>	Associate
	Phoridae	<i>Ecitophora sp.</i>	<i>Nomamyrmex esenbecki</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Phoridae	<i>Ecitophora varians</i>	<i>Eciton quadriglume</i>	Associate
	Phoridae	<i>Ecitophora varians</i>	<i>Eciton vagans</i>	Associate
	Phoridae	<i>Ecitophora varians</i>	<i>Labidus pradaetor</i>	Associate
	Phoridae	<i>Ecitoptera centralis</i>	<i>Eciton burchelli</i>	Associate
	Phoridae	<i>Ecitoptera centralis</i>	<i>Labidus coecus</i>	Associate
	Phoridae	<i>Ecitoptera concomitans</i>	<i>Eciton burchelli</i>	Associate
	Phoridae	<i>Ecitoptera concomitans</i>	<i>Eciton dulcius crassinode</i>	Associate
	Phoridae	<i>Ecitoptera concomitans</i>	<i>Eciton mexicanum</i>	Associate
	Phoridae	<i>Ecitoptera concomitans</i>	<i>Eciton vagans</i>	Associate
	Phoridae	<i>Ecitoptera concomitans</i>	<i>Nomamyrmex esenbecki</i>	Associate
	Phoridae	<i>Ecitoptera microps</i>	<i>Atta sp.</i>	Associate
	Phoridae	<i>Ecitoptera proboscidalis</i>	<i>Acromyrmex muticinodus</i>	Associate
	Phoridae	<i>Ecitoptera subciliata</i>	<i>Nomamyrmex esenbecki</i>	Associate
	Phoridae	<i>Ecitoptera subciliata</i>	<i>Eciton burchelli</i>	Associate
	Phoridae	<i>Ecitoptera subciliata</i>	<i>Eciton dulcius crassinode</i>	Associate
	Phoridae	<i>Ecitoptera subciliata</i>	<i>Eciton hamatum</i>	Associate
	Phoridae	<i>Ecitoptera subciliata</i>	<i>Eciton vagans</i>	Associate
	Phoridae	<i>Ecitoptera subciliata</i>	<i>Labidus coecus</i>	Associate
	Phoridae	<i>Ecitoptera subciliata</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Ecitoptera watkinsi</i>	<i>Neivamyrmex pilosus</i>	Associate
	Phoridae	<i>Ecituncula aptera</i>	<i>Neivamyrmex sumichrasti</i>	Associate
	Phoridae	<i>Ecituncula glandularis</i>	<i>Labidus coecus</i>	Associate
	Phoridae	<i>Ecituncula glandularis</i>	<i>Nomamyrmex esenbecki</i>	Associate
	Phoridae	<i>Ecituncula halterata</i>	<i>Eciton burchelli</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Phoridae	<i>Ecituncula halterata</i>	<i>Eciton hamatum</i>	Associate
	Phoridae	<i>Ecituncula halterata</i>	<i>Eciton vagans</i>	Associate
	Phoridae	<i>Ecituncula halterata</i>	<i>Labidus coecus</i>	Associate
	Phoridae	<i>Ecituncula halterata</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Ecituncula halterata</i>	<i>Nomamyrmex esenbecki</i>	Associate
	Phoridae	<i>Ecituncula setifrons</i>	<i>Eciton burchellii</i>	Associate
	Phoridae	<i>Ecituncula tarsalis</i>	<i>Eciton hamatum</i>	Associate
	Phoridae	<i>Ecituncula tarsalis</i>	<i>Eciton burchellii</i>	Associate
	Phoridae	<i>Ecituncula tarsalis</i>	<i>Labidus coecus</i>	Associate
	Phoridae	<i>Ecituncula tarsalis</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Hexacanterophora cohabitans</i>	<i>Dorylus nigricans</i>	Associate
	Phoridae	<i>Hexacanterophora cohabitans</i>	<i>Dorylus sp.</i>	Associate
	Phoridae	<i>Holopterina longipalpis sedula</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Homalophora attae</i>	<i>Atta sexdens</i>	Associate
	Phoridae	<i>Homalophora epichaeta</i>	<i>Eciton burchellii</i>	Associate
	Phoridae	<i>Hypogeophora macrothrix</i>	<i>Lasius sp.</i>	Associate
	Phoridae	<i>Hypogeophora macrothrix</i>	<i>Pheidole fervida</i>	Associate
	Phoridae	<i>Lenkoa aurita</i>	<i>Odontomachus affinis</i>	Associate
	Phoridae	<i>Lepidophoromyia labida</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Metopina sp.</i>	<i>Dinoponera longipipes</i>	Associate
	Phoridae	<i>Myopiomyia harmani</i>	<i>Myopias maligna</i>	Associate
	Phoridae	<i>Myriophora sp.</i>	<i>Odontomachus laticeps</i>	Associate
	Phoridae	<i>Plastophorides bequaerti</i>	<i>Pheidole rotundata</i>	Associate
	Phoridae	<i>Pradea iniqua</i>	<i>Labidus praedator</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Phoridae	<i>Psyllomyia macropygidia</i>	<i>Dorylus nigricans</i>	Associate
	Phoridae	<i>Psyllomyia macropygidia</i>	<i>Dorylus helvolus</i>	Associate
	Phoridae	<i>Psyllomyia megophthalma</i>	<i>Dorylus nigricans</i>	Associate
	Phoridae	<i>Psyllomyia patrizii</i>	<i>Dorylus sp.</i>	Associate
	Phoridae	<i>Psyllomyia sinupennata</i>	<i>Dorylus nigricans</i>	Associate
	Phoridae	<i>Pulicimyia triangularis</i>	<i>Eciton burchellii</i>	Associate
	Phoridae	<i>Puliciphora boltoni</i>	<i>Acropyga acutiventris</i>	Predator
	Phoridae	<i>Puliciphora boltoni</i>	<i>Acropyga acutiventris</i>	Predator
	Phoridae	<i>Puliciphora borinquenensis</i>	<i>Neivamyrmex sumichrasti</i>	Associate
	Phoridae	<i>Puliciphora borinquenensis</i>	<i>Eciton burchellii</i>	Associate
	Phoridae	<i>Puliciphora borinquenensis</i>	<i>Eciton dulcius crassinode</i>	Associate
	Phoridae	<i>Puliciphora borinquenensis</i>	<i>Eciton hamatum</i>	Associate
	Phoridae	<i>Puliciphora borinquenensis</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Puliciphora borinquenensis</i>	<i>Nomamyrmex esenbecki</i>	Associate
	Phoridae	<i>Puliciphora cubensis</i>	<i>Atta insularis</i>	Associate
	Phoridae	<i>Puliciphora ecitophila</i>	<i>Eciton burchellii</i>	Associate
	Phoridae	<i>Puliciphora fenestrata</i>	<i>Eciton burchellii</i>	Associate
	Phoridae	<i>Puliciphora frivola</i>	<i>Eciton burchellii</i>	Associate
	Phoridae	<i>Puliciphora imbecilla</i>	<i>Eciton burchellii</i>	Associate
	Phoridae	<i>Puliciphora karensis</i>	<i>Dorylus nigricans</i>	Associate
	Phoridae	<i>Puliciphora knighti</i>	<i>Leptogenys diminuta</i>	Associate
	Phoridae	<i>Puliciphora longipes</i>	<i>Leptogenys sp.</i>	Associate
	Phoridae	<i>Puliciphora microphthalma</i>	<i>Leptogenys ebenina</i>	Associate
	Phoridae	<i>Puliciphora nitida</i>	<i>Eciton hamatum</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Phoridae	<i>Puliciphora pulex</i>	<i>Leptogenys diminuta</i>	Associate
	Phoridae	<i>Puliciphora rata</i>	<i>Eciton burchelii</i>	Associate
	Phoridae	<i>Puliciphora rosei</i>	<i>Leptogenys mutabilis</i>	Associate
	Phoridae	<i>Puliciphora rosei</i>	<i>Leptogenys processionalis</i>	dis-Associate
			<i>tinguenda</i>	
	Phoridae	<i>Puliciphora rosei</i>	<i>Leptogenys sp.</i>	Associate
	Phoridae	<i>Puliciphora rufipes</i>	<i>Dorylus braunsi</i>	Associate
	Phoridae	<i>Puliciphora rufipes</i>	<i>Dorylus brevipennis</i>	Associate
	Phoridae	<i>Puliciphora sp.</i>	<i>Dolichoderus attelaboides</i>	Associate
	Phoridae	<i>Puliciphora sp.</i>	<i>Eciton dulcius crassinode</i>	Associate
	Phoridae	<i>Puliciphora sp.</i>	<i>Nomamyrmex esenbecki</i>	Associate
	Phoridae	<i>Rhynchomicropteron aphidiforme</i>	<i>Leptogenys sp.</i>	Associate
	Phoridae	<i>Rhynchomicropteron bifid-</i>	<i>Aenictus aratus</i>	Associate
		<i>spinarum</i>		
	Phoridae	<i>Rhynchomicropteron necadphidi-</i>	<i>Leptogenys processionalis</i>	dis-Associate
		<i>forme</i>	<i>tinguenda</i>	
	Phoridae	<i>Rhynchomicropteron necadphidi-</i>	<i>Leptogenys mutabilis</i>	Associate
		<i>forme</i>		
	Phoridae	<i>Rhynchomicropteron necbeaveri</i>	<i>Aenictus dentatus</i>	Associate
	Phoridae	<i>Rhynchomicropteron nudiventer</i>	<i>Leptogenys borneensis</i>	Associate
	Phoridae	<i>Rhynchomicropteron nudiventer</i>	<i>Leptogenys kitteli</i>	Associate
	Phoridae	<i>Rhynchomicropteron nudiventer</i>	<i>Leptogenys mutabilis</i>	Associate
	Phoridae	<i>Rhynchomicropteron nudiventer</i>	<i>Leptogenys processionalis</i>	dis-Associate
			<i>tinguenda</i>	

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Phoridae	<i>Rhynchomicropteron nudiventer</i>	<i>Aenictus laeviceps</i>	Associate
	Phoridae	<i>Rhynchomicropteron puliciforme</i>	<i>Leptogenys ocellifera</i>	Associate
	Phoridae	<i>Rhynchomicropteron puliciforme</i>	<i>Leptogenys processionalis</i>	Associate
	Phoridae	<i>Synclinusa spp.</i>	<i>Atta cephalotes</i>	Associate
	Phoridae	<i>Synclinusa spp.</i>	<i>Atta cephalotes</i>	Associate
	Phoridae	<i>Thallopтера brevisetorum</i>	<i>Eciton burchelli</i>	Associate
	Phoridae	<i>Thallopтера schwarzmaieri</i>	<i>Eciton mexicanum</i>	Associate
	Phoridae	<i>Thallopтера schwarzmaieri</i>	<i>Eciton burchelli</i>	Associate
	Phoridae	<i>Thallopтера schwarzmaieri</i>	<i>Eciton dulcius crassinode</i>	Associate
	Phoridae	<i>Thallopтера schwarzmaieri</i>	<i>Eciton hamatum</i>	Associate
	Phoridae	<i>Thallopтера schwarzmaieri</i>	<i>Eciton vagans</i>	Associate
	Phoridae	<i>Thallopтера schwarzmaieri</i>	<i>Labidus praedator</i>	Associate
	Phoridae	<i>Thallopтера sp.</i>	<i>Eciton dulcius crassinode</i>	Associate
	Phoridae	<i>Woodiphora pallidinervis</i>	<i>Odontomachus simillimus</i>	Associate
	Phoridae	<i>Xanionotum bruchi</i>	<i>Neivamyrmex gibbatus</i>	Associate
	Phoridae	<i>Xanionotum hystrix</i>	<i>Neivamyrmex carolinensis</i>	Associate
	Phoridae	<i>Xanionotum hystrix</i>	<i>Neivamyrmex nigriscens</i>	Associate
	Phoridae	<i>Xanionotum hystrix</i>	<i>Neivamyrmex opacithorax</i>	Associate
	Phoridae	<i>Xanionotum scopifer</i>	<i>Neivamyrmex sumichrasti</i>	Associate
	Phoridae	<i>Xanionotum scopifer</i>	<i>Neivamyrmex texanus</i>	Associate
	Phoridae	<i>Xanionotum wasmanni</i>	<i>Neivamyrmex gibbatus</i>	Associate
	Phoridae	<i>Xanionotum wasmanni</i>	<i>Neivamyrmex pilosus</i>	Associate
	Phoridae	<i>Xanionotum wasmanni</i>	<i>Neivamyrmex sumichrasti</i>	Associate
	Phoridae	<i>Xanionotum wasmanni</i>	<i>Neivamyrmex carolinensis</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Phoridae	<i>Xanionotum wasmanni</i>	<i>Neivamyrmex nigriscens</i>	Associate
	Phoridae	<i>Xanionotum wasmanni</i>	<i>Neivamyrmex opacithorax</i>	Associate
	Syrphidae	<i>Bardistopus papuanum</i>	<i>Technomyrmex albipes</i>	Predator
	Syrphidae	<i>Ceratophyia sp.</i>	<i>Azteca sp.</i>	Predator
	Syrphidae	<i>Masarygus planifrons</i>	<i>Camponotus mus</i>	Predator
	Syrphidae	<i>Microdon abstrusus</i>	<i>Formica exsectoides</i>	Predator
	Syrphidae	<i>Microdon albicomatus</i>	<i>Formica accreta</i>	Predator
	Syrphidae	<i>Microdon albicomatus</i>	<i>Formica aserva</i>	Predator
	Syrphidae	<i>Microdon albicomatus</i>	<i>Formica fusca</i>	Predator
	Syrphidae	<i>Microdon albicomatus</i>	<i>Formica neoclara</i>	Predator
	Syrphidae	<i>Microdon albicomatus</i>	<i>Formica neorufibarbis</i>	Predator
	Syrphidae	<i>Microdon albicomatus</i>	<i>Formica obscuripes</i>	Predator
	Syrphidae	<i>Microdon albicomatus</i>	<i>Myrmica incompleta</i>	Predator
	Syrphidae	<i>Microdon albicomatus</i>	<i>Myrmica incompleta</i>	Predator
	Syrphidae	<i>Microdon baliopterus</i>	<i>Monomorium minimum</i>	Predator
	Syrphidae	<i>Microdon cothurnatus</i>	<i>Camponotus novaeboracensis</i>	Predator
	Syrphidae	<i>Microdon cothurnatus</i>	<i>Camponotus pennsylvanicus</i>	Predator
	Syrphidae	<i>Microdon cothurnatus</i>	<i>Camponotus vicinus</i>	Predator
	Syrphidae	<i>Microdon cothurnatus</i>	<i>Formica accreta</i>	Predator
	Syrphidae	<i>Microdon cothurnatus</i>	<i>Formica adamsi whymperi</i>	Predator
	Syrphidae	<i>Microdon cothurnatus</i>	<i>Formica aserva</i>	Predator
	Syrphidae	<i>Microdon cothurnatus</i>	<i>Formica neoclara</i>	Predator
	Syrphidae	<i>Microdon cothurnatus</i>	<i>Formica obscuripes</i>	Predator
	Syrphidae	<i>Microdon cothurnatus</i>	<i>Formica obscuriventris</i>	Predator

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Syrphidae	<i>Microdon cothurnatus</i>	<i>Formica podzolica</i>	Predator
	Syrphidae	<i>Microdon cothurnatus</i>	<i>Formica ravidia</i>	Predator
	Syrphidae	<i>Microdon fulgens</i>	<i>Camponotus atriceps</i>	Predator
	Syrphidae	<i>Microdon fulgens</i>	<i>Polyergus lucidus</i>	Predator
	Syrphidae	<i>Microdon fuscipennis</i>	<i>Forelius pruinosus</i>	Predator
	Syrphidae	<i>Microdon globosus</i>	<i>Tapinoma sessile</i>	Predator
	Syrphidae	<i>Microdon katsurai</i>	<i>Polyrhachis lamellidens</i>	Predator
	Syrphidae	<i>Microdon kidai</i>	<i>Formica japonica</i>	Predator
	Syrphidae	<i>Microdon lanceolatus</i>	<i>Formica argentea</i>	Predator
	Syrphidae	<i>Microdon lanceolatus</i>	<i>Formica neogagates</i>	Predator
	Syrphidae	<i>Microdon macrocerus</i>	<i>Camponotus obscuripes</i>	Predator
	Syrphidae	<i>Microdon manitobensis</i>	<i>Formica densiventris</i>	Predator
	Syrphidae	<i>Microdon manitobensis</i>	<i>Formica neoclara</i>	Predator
	Syrphidae	<i>Microdon megalogaster</i>	<i>Formica subsericea</i>	Predator
	Syrphidae	<i>Microdon murayami</i>	<i>Formica lemani</i>	Predator
	Syrphidae	<i>Microdon mutabilis</i>	<i>Lasius niger</i>	Predator
	Syrphidae	<i>Microdon mutabilis</i>	<i>Formica lemani</i>	Predator
	Syrphidae	<i>Microdon mutabilis</i>	<i>Leptothorax sp.</i>	Predator
	Syrphidae	<i>Microdon myrmicae</i>	<i>Myrmica scabrinodis</i>	Predator
	Syrphidae	<i>Microdon ocellaris</i>	<i>Formica schaufussi</i>	Predator
	Syrphidae	<i>Microdon pipieri</i>	<i>Camponotus herculeanus</i>	Predator
	Syrphidae	<i>Microdon pipieri</i>	<i>Camponotus modoc</i>	Predator
	Syrphidae	<i>Microdon pipieri</i>	<i>Camponotus sp.</i>	Predator
	Syrphidae	<i>Microdon pipieri</i>	<i>Camponotus vicinus</i>	Predator

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Syrphidae	<i>Microdon pipieri</i>	<i>Formica accreta</i>	Predator
	Syrphidae	<i>Microdon pipieri</i>	<i>Formica adamsi whymperi</i>	Predator
	Syrphidae	<i>Microdon pipieri</i>	<i>Formica aserva</i>	Predator
	Syrphidae	<i>Microdon pipieri</i>	<i>Formica neoclara</i>	Predator
	Syrphidae	<i>Microdon pipieri</i>	<i>Formica neorufibarbis</i>	Predator
	Syrphidae	<i>Microdon pipieri</i>	<i>Formica obscuripes</i>	Predator
	Syrphidae	<i>Microdon pipieri</i>	<i>Formica obscuriventris</i>	Predator
	Syrphidae	<i>Microdon pipieri</i>	<i>Formica ravidia</i>	Predator
	Syrphidae	<i>Microdon ruficrus</i>	<i>Lasius alienus</i>	Predator
	Syrphidae	<i>Microdon ruficrus</i>	<i>Lasius sp.</i>	Predator
	Syrphidae	<i>Microdon sp.</i>	<i>Formica fusca</i>	Predator
	Syrphidae	<i>Microdon sp.</i>	<i>Formica rufa</i>	Predator
	Syrphidae	<i>Microdon sp.</i>	<i>Formica rufibarbis</i>	Predator
	Syrphidae	<i>Microdon sp.</i>	<i>Formica sanguinea</i>	Predator
	Syrphidae	<i>Microdon sp.</i>	<i>Lasius brunneus</i>	Predator
	Syrphidae	<i>Microdon sp.</i>	<i>Lasius flavus</i>	Predator
	Syrphidae	<i>Microdon sp.</i>	<i>Lasius fuliginosus</i>	Predator
	Syrphidae	<i>Microdon sp.</i>	<i>Lasius niger</i>	Predator
	Syrphidae	<i>Microdon sp.</i>	<i>Ectatomma ruidum</i>	Predator
	Syrphidae	<i>Microdon sp.</i>	<i>Lasius pallitarsis</i>	Predator
	Syrphidae	<i>Microdon triginus</i>	<i>Acromyrmex coronatus</i>	Predator
	Syrphidae	<i>Microdon tristis</i>	<i>Camponotus novaeboracensis</i>	Predator
	Syrphidae	<i>Microdon tristis</i>	<i>Camponotus pennsylvanicus</i>	Predator
	Syrphidae	<i>Microdon tristis</i>	<i>Formica aserva</i>	Predator

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Syrphidae	<i>Microdon tristis</i>	<i>Formica difficilis</i>	Predator
	Syrphidae	<i>Microdon tristis</i>	<i>Formica obscuripes</i>	Predator
	Syrphidae	<i>Microdon tristis</i>	<i>Formica schaufussi</i>	Predator
	Syrphidae	<i>Microdon waterhousei</i>	<i>Polyrhachis sp.</i>	Predator
	Syrphidae	<i>Microdon xanthopilis</i>	<i>Formica obscuripes</i>	Predator
	Syrphidae	<i>Microdon yokohamai</i>	<i>Formica japonica</i>	Predator
	Syrphidae	<i>Mixogaster lanei</i>	<i>Linepithema humile</i>	Predator
	Syrphidae	<i>Oligeriops dimorphon</i>	<i>Iridomyrmex chasei</i>	Predator
	Syrphidae	<i>Oligeriops iridomyrmex</i>	<i>Iridomyrmex rufoniger</i>	Predator
	Syrphidae	<i>Omegasyrphus baliopterus</i>	<i>Monomorium minimum</i>	Predator
	Syrphidae	<i>Omegasyrphus coarctatus</i>	<i>Aphaenogaster fulva</i>	Predator
	Syrphidae	<i>Omegasyrphus coarctatus</i>	<i>Monomorium minimum</i>	Predator
	Syrphidae	<i>Omegasyrphus painteri</i>	<i>Monomorium minimum</i>	Predator
	Syrphidae	<i>Paramixogaster acantholepidis</i>	<i>Lepisiota capensis</i>	Predator
	Syrphidae	<i>Paramixogaster crematogastri</i>	<i>Crematogaster sp.</i>	Predator
	Syrphidae	<i>Pseudomicrodon biluminiferus</i>	<i>Crematogaster limata</i>	Predator
	Syrphidae	<i>Rhopalosyrphus ramulorum</i>	<i>Pseudomyrmex ejectus</i>	Predator
	Syrphidae	<i>Rhopalosyrphus ramulorum</i>	<i>Pseudomyrmex simplex</i>	Predator
	Syrphidae	<i>Serichlamys</i>	<i>Pheidole dentata</i>	Predator
	Syrphidae	<i>Stipomorpha sp.</i>	<i>Crematogaster sp.</i>	Predator
	Syrphidae	<i>Stipomorpha wheeleri</i>	<i>Crematogaster crinosa</i>	Predator
	Tachinidae	<i>Androeryops ecitonis</i>	<i>Eciton burchelii</i>	Associate
	Tachinidae	<i>Androeryops ecitonis</i>	<i>Labidus praedator</i>	Associate
	Tachinidae	<i>Calodexia agilis</i>	<i>Eciton burchelii</i>	Associate

Continuation of Table A.2

Group	Associate family	Associate species	Ant species	Relationship
	Tachinidae	<i>Calodexia bella</i>	<i>Eciton burchelii</i>	Associate
	Tachinidae	<i>Calodexia continua</i>	<i>Eciton burchelii</i>	Associate
	Tachinidae	<i>Calodexia dives</i>	<i>Eciton burchelii</i>	Associate
	Tachinidae	<i>Calodexia fasciata</i>	<i>Eciton burchelii</i>	Associate
	Tachinidae	<i>Calodexia fumosa</i>	<i>Eciton burchelii</i>	Associate
	Tachinidae	<i>Calodexia interupta</i>	<i>Eciton burchelii</i>	Associate
	Tachinidae	<i>Calodexia major</i>	<i>Eciton burchelii</i>	Associate
	Tachinidae	<i>Calodexia panamensis</i>	<i>Eciton burchelii</i>	Associate
	Tachinidae	<i>Calodexia similis</i>	<i>Eciton burchelii</i>	Associate
	Tachinidae	<i>Calodexia varia</i>	<i>Eciton burchelii</i>	Associate
	Tachinidae	<i>Calodexia venteris</i>	<i>Eciton burchelii</i>	Associate

End of Table A.2

B

Supplementary Information for Chapter 3

B.1 Model Parameters

A description of the model parameters and their values are given in Table 3.1. Whenever possible, estimates of model parameters were extracted from published values. Here we provide a detailed discussion of how model parameter values were chosen, and summarize empirical estimates from the literature in Tables B.1 B.2a, B.2b, B.3, B.4, B.5, B.6, B.7.

Colony birth rate λ

For colony birth rate, there is a large range in published values in the literature. This is due to large differences between ant species, with some species having extremely large colony sizes and thus large numbers of eggs laid per day while other species have small colonies and smaller birth rates (Table B.1). In our model, the overall rate at which new brood are born into the colony is dependent on the colony birth rate parameter λ , the current colony population ($F_s + F_i + N + B$), the minimum colony size σ needed to maintain colony viability, and this together is modulated via a Hill function (see Eq. 3.1). We explore a range of colony birthrates to assess the impact of the λ parameter on colony dynamics under the presence of *ex-nido* parasites (Fig. 3.4).

Brood - nest worker transition rate ϕ .

For the brood-nest worker transition rate, ϕ , the range in this parameter is due to the impacts of temperature on brood development time, with values of 18 days to 180 days reported in the literature (Tables B.2a, B.2b). For simplicity, we assume a constant transition rate with value $1/56 \text{ days}^{-1}$, the inverse of the median brood development times reported in the literature.

Nest worker - forager transition α and κ

The nest worker-forager transition is governed by two parameters in our model: κ (the maximum proportion of the colony that are foragers), which dictates how many new foragers need to be recruited from the nest worker compartment, and α , the maximal rate at which the nest worker-forager transition occurs in the absence of foragers. Estimates of the proportion of ant colony populations that engage in foraging are scarce (Table B.3), and the estimates that have been reported vary considerably, ranging between 4.5 - 90%. It is likely that the proportion of the colony that foragers changes seasonally, but for model simplicity we make the assumption that a maximum of thirty percent of the colony is in the forager compartment at any given time. We explore how sensitive colony population dynamics are to changing this forager proportion κ under the presence of *ex-nido* parasitism in Fig. 3.5. We also perform sensitivity analyses for predicted colony dynamics under changing α in Fig. B.4.

Natural mortality rate μ

Our understanding of natural mortality rates and worker lifespan in ants is limited by the relative difficulty of following individuals over the course of their lifetime under field settings. Accordingly, most estimates of worker lifespan come from laboratory studies, which preclude many natural causes of death (i.e. predation, interspecific competition and aggression, and parasitism). Worker life spans greater than one year have been reported for several species (Table B.4), with some exceeding three years. For studies that have followed worker life spans in the field, the life spans of ants once they become foragers are far less (6 - 30 days). For simplicity, we assume an individual's lifespan to be 1 year, which corresponds to a natural mortality rate of $1/365 \text{ days}^{-1}$. We assume that each compartment has the same natural mortality rate; we explore

the effects of changing the natural mortality rate in Fig. B.2.

Parasite-induced mortality rate γ

In our model, we assume that successful infection leads to mortality, thus we define parasite-induced mortality rate as the rate at which infected individuals die, not their probability of dying. Few estimates of parasite-induced mortality rates for parasites of social insects exist in the literature. We summarize reported estimates of the inverse survival time in Table B.5 and formally explore the impacts of changing the parasite-induced mortality rate in Fig. B.3.

B.2 Additional modeling results

Changing the nest worker - forager transition term α

Changing the nest-forager transition term α does not qualitatively change either the transient or equilibrium dynamics for the model (Fig. B.4). An α of 0.1 leads to a percent reduction of approximately 46% relative to the uninfected model, whereas an α of 1.0 leads to a percent reduction of approximately 50% (Fig. B.4), so the model is not very sensitive to changes in α within biologically reasonable ranges. Altering α slightly modifies how quickly nest workers transition into the forager compartment depending on colony need (i.e. to make up the difference between the number of foragers present and the foraging cap κ). Smaller α indicates that the transition to fill the forager compartment occurs more slowly; this results in slightly fewer foragers being in the compartment leading to fewer individuals being at risk of becoming parasitized and thus a slightly reduced percent reduction in total colony size.

B.3 Additional Discussion

Please refer to the main text for a complete discussion of the results of this study. Here we present additional discussion fodder for interested readers.

The force of infection parameter β

The results of our model show that the force of infection parameter β is extremely important for predicting the severity of the impact of indirectly transmitting parasites on total colony size. The β parameter is composed of three different parameters: the rate at which individuals forage, the rate at which foragers encounter parasites in the extranidal environment while foraging, and the probability that an encounter with a parasite while foraging becomes a successful infection. For all three components of β , few if any empirical estimates are known. While work has been done on colony-wide foraging ranges and rates [505,506], the frequency with which a given individual forages has been measured only a handful of times [507–510]. Studies investigating individual foraging rates suggest that most foragers make few trips while a small proportion of foragers make many trips [507], which would lead to heterogeneity in infection risk. It is also important to acknowledge that non-foragers can also be periodically exposed to the extranidal environment and thus to parasite exposure. For example, in nomadic ant species such as those in the army ant tribe Ecitonini, frequent nest relocation could expose brood and intranidal workers as well. How such host ecological traits relate to parasitism pressure will be the subject of future work.

The second component of β , how frequently parasites are encountered in the extranidal environment, remains enigmatic. For the vast majority of parasites infecting social insects, we have no idea how frequently potential hosts encounter infective stages such as fungal spores, largely due to the inherent difficulties in gathering such data. Some work has investigated the attack rates of parasitoids and found that attack rates can vary with host density and distance from nests [511] as well as with the number of host species in the area [512]. For the ant fungal parasite *Ophiocordyceps unilateralis s.l.*, infected cadavers have been behaviorally manipulated to die above foraging trails at the doorstep of the colony [231], where they can rain spores down on foragers as they leave the nest. However, these cadavers have been shown to have temporal windows over which spores are released and as foragers continue to walk over trails spores are effectively ‘cleaned up’, suggesting variable individual encounter rates. Thus, while information on actual encounter rates is scarce, heterogeneity appears to be likely in how frequently social insect hosts encounter parasites in the extranidal environment.

The third component of β - how often parasite encounters lead to successful

infection - is also relatively unknown, but host behavior and the effects of social immunity could serve to significantly reduce actual parasitism rates. When parasitoid flies are present, ants have been shown to reduce their foraging behaviour in response [428, 513, 514] and leaf-cutter ants even have workers who defend foragers from parasitoid attacks [515]. For individuals that have picked up fungal spores or infective larval stage helminths, allogrooming and self-grooming can be effective strategies to prevent actual infection [125, 133, 139, 516, 517]. Other mechanisms of social immunity, such as the spraying of formic acid and use of metapleural gland secretions [121, 122] can also kill parasites before infection can commence.

Taken together, what information we do have on the above components of β suggests that the infective pressure of parasites is probably quite heterogeneous. Thus, our model, which uses a constant rate of parasite infection likely overestimates the impact of indirect parasite pressure on the reduction of colony population numbers. Better empirical estimates of the components of β are needed to truly identify the impact *ex-nido* parasites might have on colony populations.

Impacts of worker loss on colony functioning and fitness

This work has explored how the presence of indirect parasites could impact colony population dynamics, but how such potential population reductions translate into impacts on colony fitness remains an open question. Does a 10% reduction in colony population lead to a 10% reduction in colony fitness? This seems unlikely but empirical data are scant. Also, are colonies able to functionally buffer the loss of individuals through redundancies in their social organization? Indirect parasites, by modifying host behavior (i.e. reduced foraging in the presence of parasitoids [428], can also potentially impact colonies in nuanced ways that are subtler than simple reductions in colony size. Better understanding of the link between colony size, social structure, functioning, and fitness will allow us to better understand the interaction of social insects and their parasites in an evolutionary context.

The impact of worker loss might manifest in other ways besides colony growth or the production of reproductives. Increasing evidence shows that there are important individual differences in task performance and personality [518], and these differences can cascade up to alter colony-level organization and phenotypes [473, 519]. Thus, the parasite-induced loss of 'keystone' individuals could potentially alter colony pheno-

type, with downstream consequences for colony competitive ability and thus growth, survival, and reproduction.

An additional way that the parasite-induced loss of workers could impact colonies is by promoting a positive feedback between worker loss and future parasitism events if, for example, inexperienced foragers had to make more trips or encountered more parasites in the environment than the experienced foragers that they replaced. While our model does not include this potential feedback, it would be interesting to examine both theoretically and empirically.

Impacts of parasites that cause morbidity rather than mortality

For modeling simplicity, we have only included parasite records where the parasite clearly caused mortality for the infected individual. We have excluded parasites that cause sickness behaviour rather than mortality, or where the exact extent of host pathology is unclear. The colony-level impact of these parasites causing morbidity merits further investigation.

Need for more empirical measurements of ant colony sociometry

The modeling approach employed in this work has been useful for clarifying what host biological features might be the most important for colony survival while in the presence of indirect parasites. While some parameter estimates were easily gleaned from published studies (i.e. brood developmental time), other important parameters such as colony birth rate and the proportion of the colony work force dedicated to foraging have far less empirical data available. In order to more accurately model how colonies grow in the presence of absence of parasitism and to validate this current model, we need better estimates of basic ant colony sociometry, as has been advocated by Tschinkel [520].

B.4 Figures and Tables

Figure B.1: Recovery dynamics from the uninfected model in the face of perturbation.

Recovery dynamics (from numerical simulation) for the uninfected model (eqs. 1-3) under baseline parameter values given in Table 3.1. Initial colony conditions were set at $F_s = 200$ ants, $N = 500$ ants, and $B = 100$ ants and the colony was allowed to go to equilibrium. At $t = 5,000$ days, the colony size was reduced by 50%, 80%, or 90% (applied across all compartments) and allowed to return to equilibrium.

Recovery from colony perturbation in the uninfected model ($\beta = 0 \text{ days}^{-1}$)

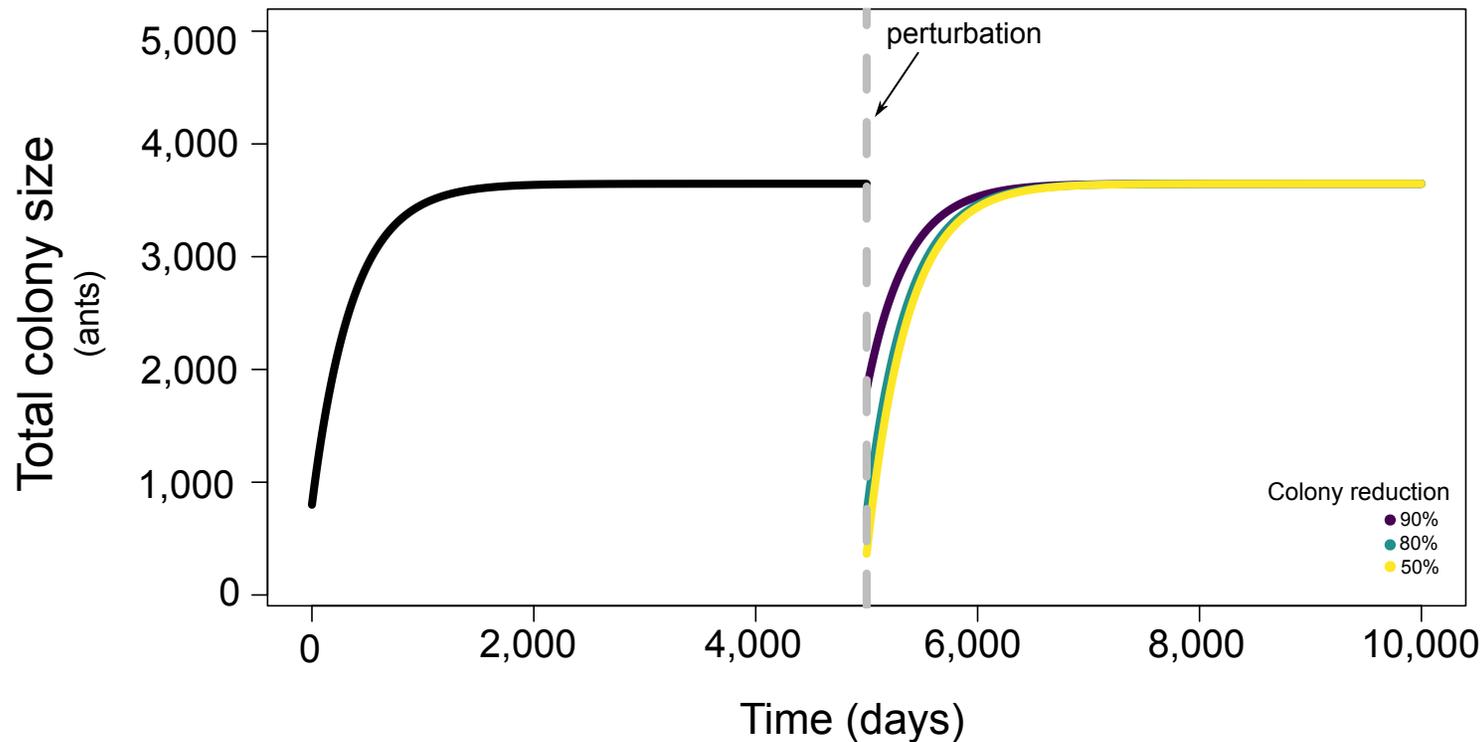


Figure B.2: Sensitivity of model predictions to changing the natural mortality rate, μ .

Model predictions are from numerical simulation under baseline parameter values given in Table 3.1. (a) The proportion reduction in colony size relative to the uninfected model under changing values of μ from 0 to 0.1 days^{-1} . (b) Total colony size (Fs + N + B) under changing values of μ from 0 to 0.1 days^{-1} .

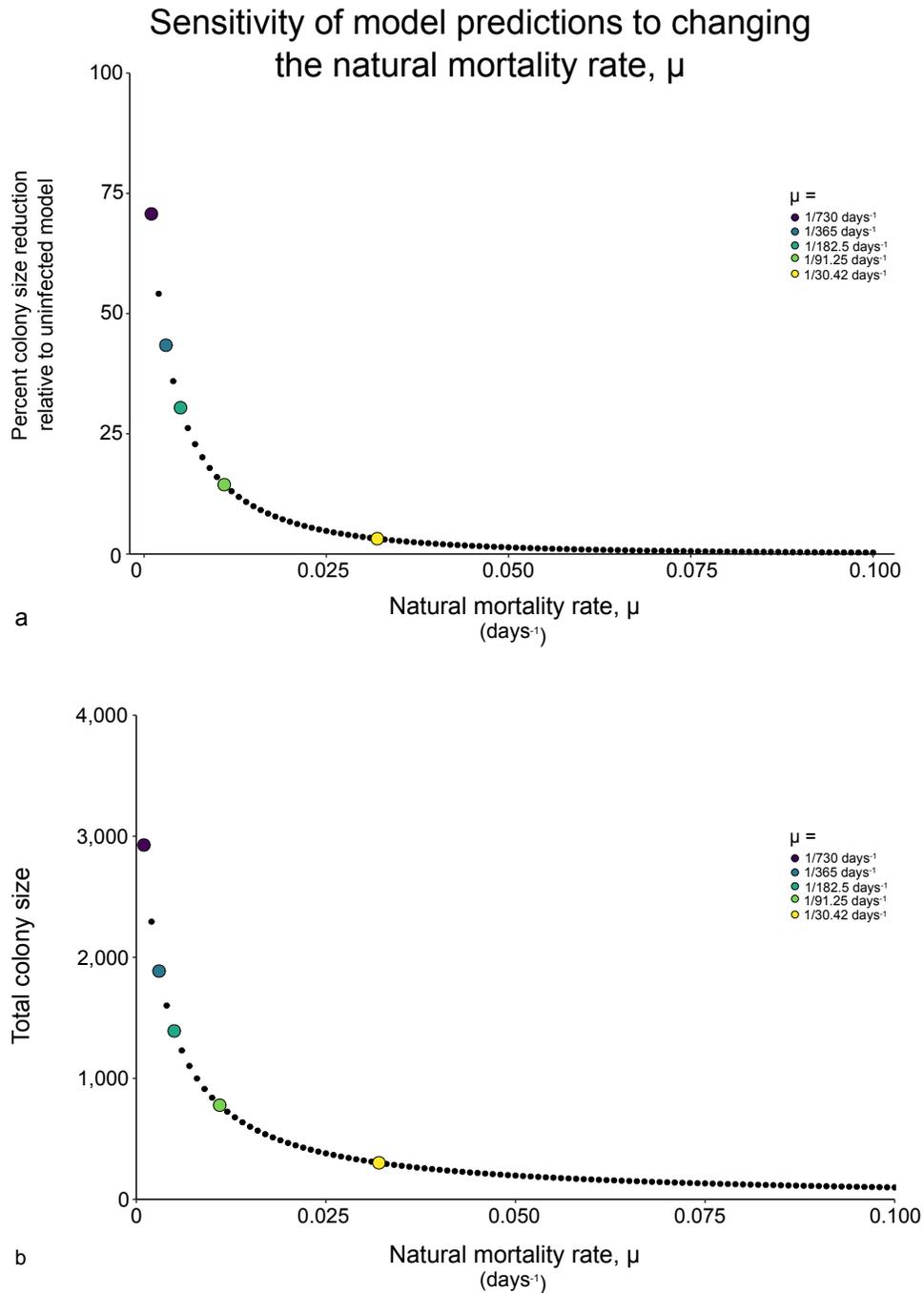


Figure B.3: Sensitivity of model predictions to changing the parasite-induced mortality rate, γ .

Model predictions are from numerical simulation under baseline parameter values given in Table 3.1. (a) The proportion reduction in colony size relative to the uninfected model under changing values of γ from 0 to 1 days⁻¹. (b) Total colony size ($F_s + N + B$) under changing values of γ from 0 to 1 days⁻¹.

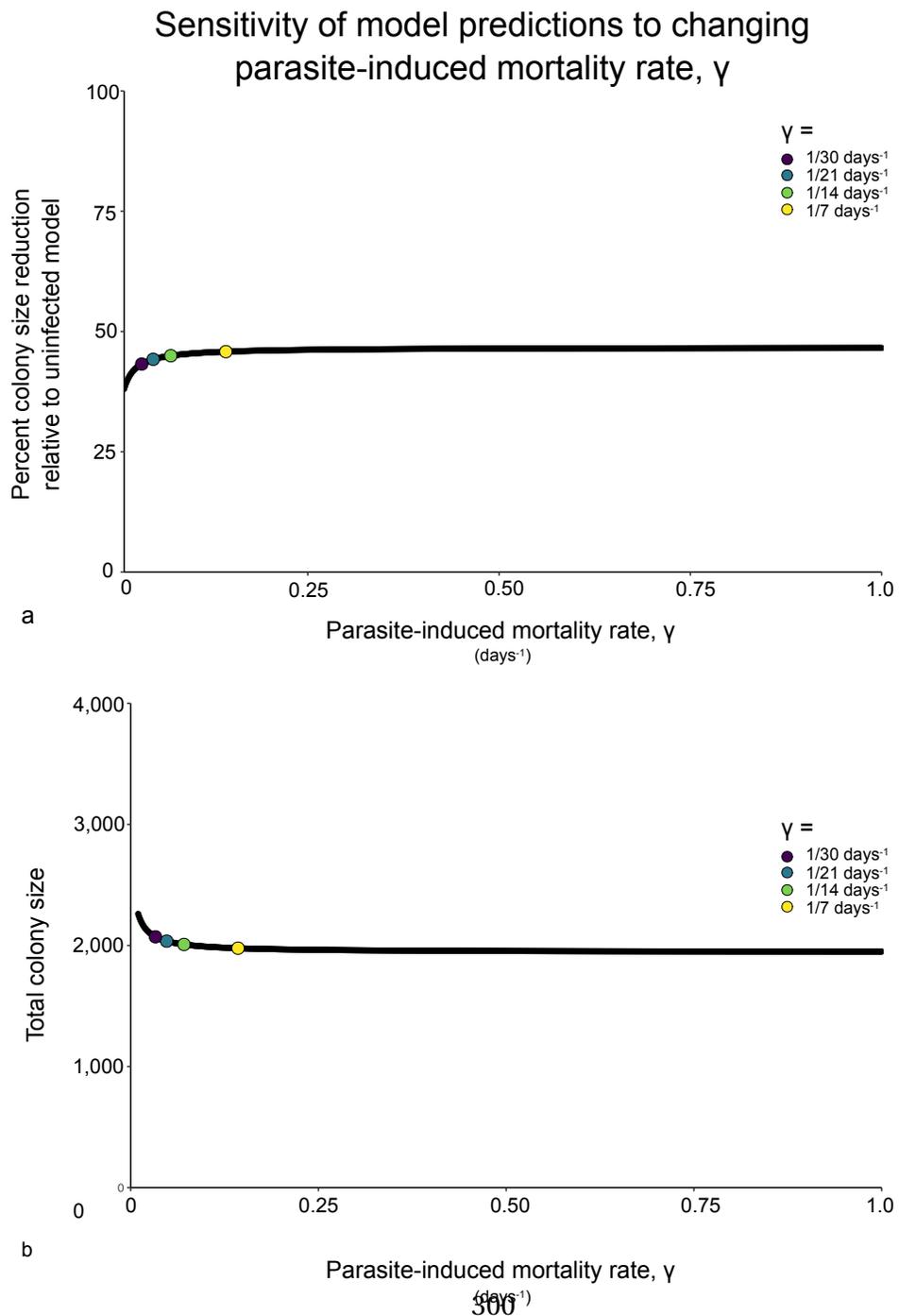


Figure B.4: Sensitivity of model predictions to changing the nest worker → forager transition term, α .

Model predictions are from numerical simulation under baseline parameter values given in Table 3.1. (a) The proportion reduction in colony size relative to the uninfected model under changing values of α from 0 to 1. (b) Total colony size ($F_s + N + B$) under changing values of α from 0 to 1.

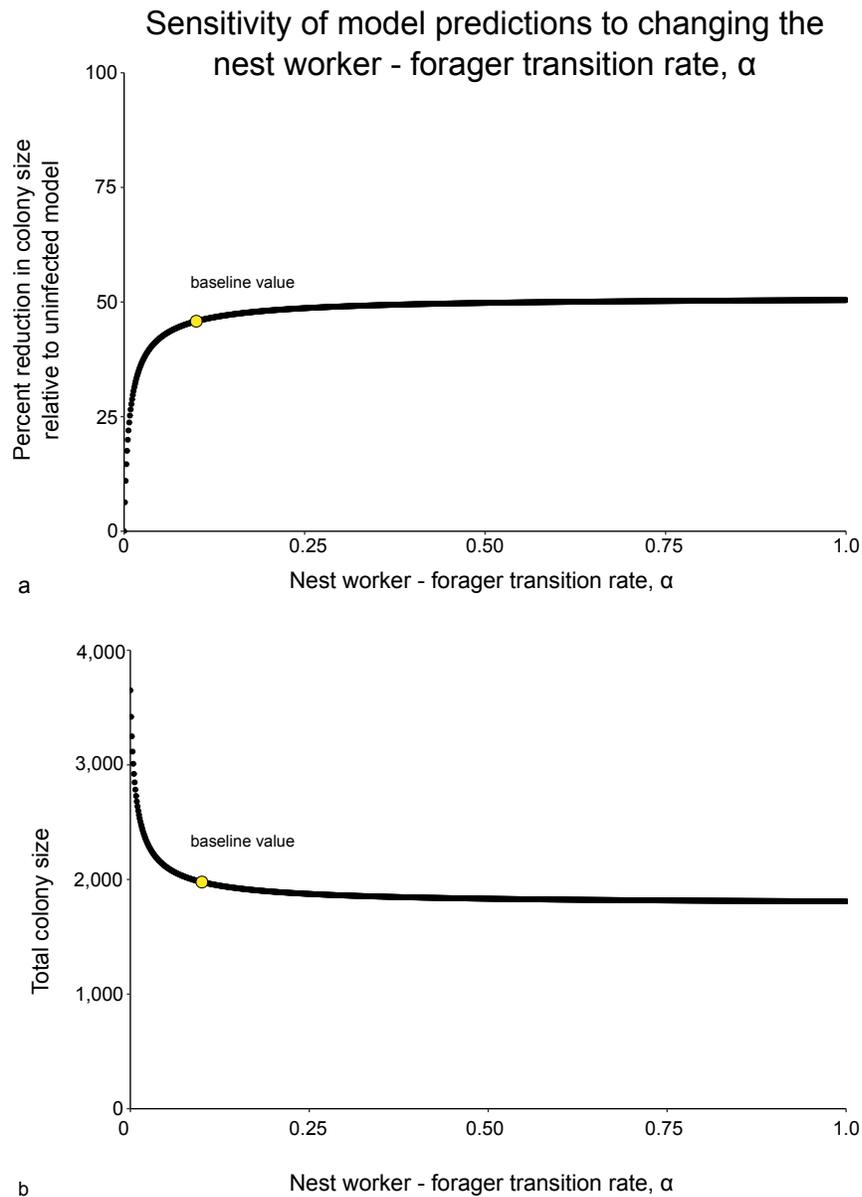


Figure B.5: Impact of seasonality in parasite force of infection on model predictions (one annual peak).

Model predictions are from numerical simulation under baseline parameter values given in Table 3.1. (a) The proportion reduction in colony size relative to the uninfected model under different maximum values of β with one annual peak. (b) Total colony size ($F_s + N + B$) under different maximum values of β with one annual peak.

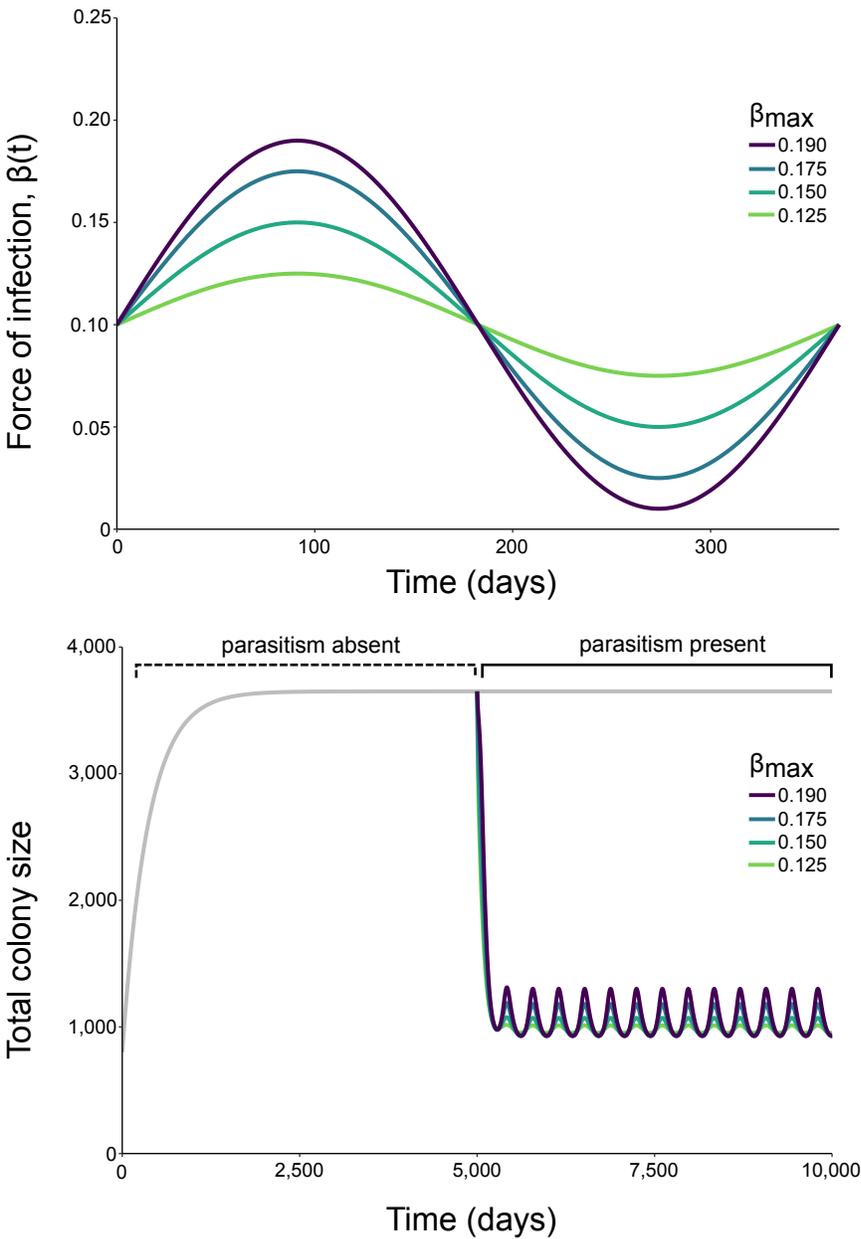


Figure B.6: Impact of seasonality in parasite force of infection on model predictions (two annual peaks).

Model predictions are from numerical simulation under baseline parameter values given in Table 3.1. (a) The proportion reduction in colony size relative to the uninfected model under different maximum values of β with two annual peaks. (b) Total colony size ($F_s + N + B$) under different maximum values of β with two annual peaks.

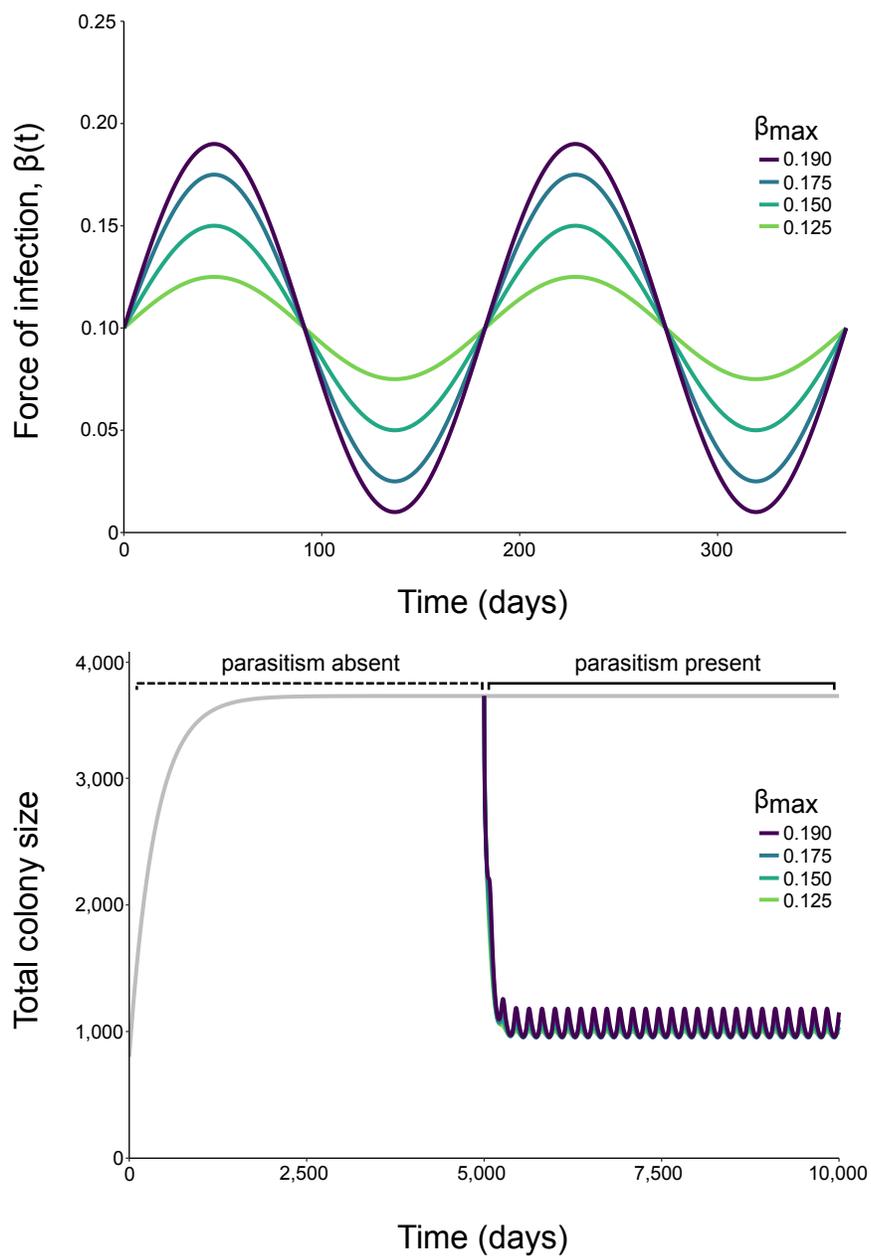


Table B.1: Parameter estimates from the literature: colony birth rate

Colony birth rate, λ			
Ant species	Birth rate	Notes	Reference
<i>Solenopsis invicta</i>	0 - 50 workers/day	Varies seasonally.	[521]
<i>Lasius neglectus</i>	6 - 14 eggs/day/queen	-	[522]
<i>Solenopsis invicta</i>	62 - 1776 eggs/day	Depends on the number of larvae already in the nest	[420]
<i>Leptothorax acervorum</i>	1 - 23 eggs/day	-	[523]
<i>Dolichoderus mariae</i>	27 - 40 eggs/day/queen	-	[524]
<i>Dolichoderus mariae</i>	1500 - 6000 eggs/day/nest	-	[524]
<i>Iridomyrmex purpureus</i>	93 - 175 eggs/day/queen	Depends on queen's rank dominance	[525]

Table B.2a: Parameter estimates from the literature: brood developmental rate

Brood developmental rate $1/\phi$				
Ant species	Avg. time to adult emergence (days)	Range (days)	Reference	Notes
<i>Solenopsis invicta</i>	18	-	[526]	-
<i>Linepithema humile</i>	-	40 - 140	[527]	-
<i>Solenopsis invicta</i>	-	23 - 55	[528]	-
<i>Solenopsis invicta</i>	-	20 - 31	[529]	-
<i>Dinoponera quadriceps</i>	95	90 - 100	[530]	within [531]
<i>Myrmecia regularis</i>	-	150 - 180	[532]	within [531]
<i>Tetraponera anthracina</i>	100	-	[533]	within [531]
<i>Aenictus laeviceps</i>	65	-	[15]	within [531]
<i>Eciton burchelli</i>	45	-	[50]	within [531]
<i>Eciton hamatum</i>	50	-	[15]	within [531]
<i>Atta sexdens</i>	-	40 - 60	[534]	within [531]
<i>Messor aciculatus</i>	69.3	-	[535]	within [531]
<i>Messor pergandei</i>	60	-	[536]	within [531]
<i>Myrmica rubra</i>	115	-	[537]	within [531]
<i>Myrmica rubra</i>	84	-	[537]	within [531]
<i>Myrmica rubra</i>	54	-	[537]	within [531]
<i>Monomorium pharaonis</i>	36.4	-	[538]	within [531]
<i>Monomorium pharaonis</i>	-	25 - 54	[539]	within [531]
<i>Pogonomyrmex sp.</i>	-	35 - 42	[540]	within [531]
<i>Solenopsis invicta</i>	-	24 - 25	[541]	within [531]
<i>Solenopsis invicta</i>	-	55	[528]	within [531]
<i>Tetramorium caespitum</i>	-	43 - 63	[542]	within [531]
<i>Linepithema humile</i>	44	-	[543]	within [531]

Table B.2b: Parameter estimates from the literature

Table B.2, continued.

Brood developmental rate $1/\phi$				
Ant species	Avg. time to adult emergence (days)	Range (days)	Reference	Notes
<i>Wasmannia auropunctata</i>	-	35 - 40	[544]	within [531]
<i>Liometopum apiculatum</i>	28.2	-	[545]	within [531]
<i>Liometopum apiculatum</i>	70.8	-	[545]	within [531]
<i>Camponotus clariothorax</i>	67	-	[546]	within [531]
<i>Camponotus festinatus</i>	69	-	[546]	within [531]
<i>Camponotus laevigatus</i>	-	48 - 70	[546]	within [531]
<i>Camponotus modoc</i>	55	-	[546]	within [531]
<i>Camponotus planatus</i>	57	54 - 58	[546]	within [531]
<i>Camponotus sericeus</i>	-	24 - 26	[547]	within [531]
<i>Camponotus sericeus</i>	55	-	[547]	within [531]
<i>Camponotus sericeus</i>	20	-	[547]	within [531]
<i>Camponotus vicinus</i>	-	54 - 70	[546]	within [531]
<i>Formica polyctena</i>	-	35 - 45	[548]	within [531]
<i>Formica rufa</i>	-	35 - 37	[549]	within [531]
<i>Oecophylla longinoda</i>	39	-	[550]	within [531]
<i>Prenolepis imparis</i>	-	70 - 90	[551]	within [531]

Table B.3: Parameter estimates from the literature: proportion of the colony foraging

Proportion of the colony that forages, κ			
Ant species	% that are foragers	Notes	Reference
<i>Formica polyctena</i>	4.5 - 57.5%	-	[552]
<i>Solenopsis invicta</i>	16 - 58%	-	[412]
<i>Pogonomyrmex owyheeii</i>	16%	-	[553]
<i>Pogonomyrmex badius</i>	5 - 42%	-	[415]
<i>Solenopsis invicta</i>	10 - 90%	-	[554]
<i>Solenopsis invicta</i>	30 - 80%	-	[554]
<i>Pogonomyrmex mendozanus</i>	10 - 13%	-	[555]
<i>Pogonomyrmex inermis</i>	15 - 44%	-	[555]
<i>Pogonomyrmex rastratus</i>	7 - 10%	-	[555]

Table B.4: Parameter estimates from the literature: natural mortality rate

Natural mortality rates, μ , of workers (not reproductives)			
Ant species	Avg. life span (days)	Notes	Reference
<i>Atta colombica</i>	3 - 4 days	Avg. lifespan for 50% surviving	[556]
<i>Cataglyphis bicolor</i>	6 days	-	[557]
<i>Pogonomyrmex owyheeii</i>	14 days	-	[553]
<i>Pogonomyrmex sp.</i>	30 days	-	[558]
<i>Solenopsis invicta</i>	60 - 540 days	-	[559]
<i>Solenopsis invicta</i>	70 - 490	-	[560]
<i>Oecophylla smaragdina</i>	175 - 210 days	Avg. lifespan for 50% surviving	[561]
<i>Aphaenogaster rudis</i>	> 1095 days	Maximum recorded.	[562], within [5].
<i>Leptothorax lichtensteini</i>	912 days	-	[563], within [5].
<i>Leptothorax nylanderi</i>	1095 days	-	[563], within [5].
<i>Monomorium pharaonis</i>	63 - 70 days	-	[538], within [5].
<i>Myrmecia gulosa</i>	620 days	-	[564], within [5].
<i>Myrmecia nigriceps</i>	803 days	-	[564], within [5].
<i>Myrmecia nigrocinta</i>	438 days	-	[564], within [5].
<i>Myrmecia pilosula</i>	474 days	-	[564], within [5].
<i>Myrmecia vindex</i>	693 days	-	[564], within [5].
<i>Rhytidoponera purpurea</i>	949 days	-	[564], within [5].
<i>Platythyrea punctata</i>	100 - 200 days	-	[565]
<i>Lasius niger</i>	325 days	Avg. lifespan for 50% surviving, control treatment	[566]
<i>Diacamma rugosum</i>	208.8 days	-	[567]

Table B.5: Parameter estimates from the literature: parasite-induced mortality rates

Parasite-induced mortality rate, γ						
Parasite species	Trans. location	lo-	Avg. development time	develop-	Notes	Reference
<i>Ophiocordyceps unilateralis</i>	<i>Ex-nido</i>		6 - 20 days		-	[255]
<i>Beauveria bassiana</i>	<i>In-nido</i>		3 - 7 days		-	[438]
<i>Metarhizium anisopliae</i>	<i>In-nido</i>		10 - 30 days		Varies based on colony genetic diversity: polygynous vs. monogynous	[568]
<i>Metarhizium anisopliae</i>	<i>In-nido</i>		3 - 9 days		-	[125]
<i>Pseudacteon litoralis</i>	<i>Ex-nido</i>		46 days		For larval + pupal development inside ant	[417]
<i>Pseudacteon litoralis</i>	<i>Ex-nido</i>		30 - 49 days		For larval + pupal development inside ant	[569]
<i>Pseudacteon tricuspis</i>	<i>Ex-nido</i>		23 - 50 days		For larval + pupal development inside ant	[569]
<i>Pseudacteon browni</i>	<i>Ex-nido</i>		23 - 43 days		For larval + pupal development inside ant	[569]
<i>Pseudacteon crawfordi</i>	<i>Ex-nido</i>		24 - 32 days		For larval + pupal development inside ant	[569]

Table B.6: Parameter estimates from the literature: foraging rates

Foraging rate, a component of β			
Ant species	Avg. foraging trips/day per ant	Notes	Reference
<i>Pogonomyrmex barbatus</i>	1 - 25 (24 hrs)	-	[510]
<i>Paraponera clavata</i>	1 - 9 (12 hrs)	-	[508]
<i>Cataglyphis bicolor</i>	3.7 (24 hrs)	-	[509]
<i>Pogonomyrmex montanus</i>	50 - 950 trips/day per colony	Reported as mean foraging trips per day for entire colonies, not for individual foragers. Number of foraging trips/day/colony varies seasonally.	[540]
<i>Pogonomyrmex subnitidus</i>	50 - 10,500 trips/day per colony	Reported as mean foraging trips per day for entire colonies, not for individual foragers. Number of foraging trips/day/colony varies seasonally.	[540]
<i>Pogonomyrmex rugosus</i>	50 - 25,000 trips/day per colony	Reported as mean foraging trips per day for entire colonies, not for individual foragers. Number of foraging trips/day/colony varies seasonally.	[540]

Table B.7: Parameter estimates from the literature: parasite encounter rates

Parasite encounter rate, a component of β			
Ant species	Parasite	Attack rate	Reference
<i>Linepithema sp.</i>	<i>Pseudacteon sp.</i>	No direct attack rates provided, but see results section.	[512]
<i>Azteca instabilis</i>	<i>Pseudacteon sp.</i>	0 - 8 attacks/15 mins	[570]
<i>Atta vollenweideri, Acromyrmex sp.</i>	Various	0.3 - 1.2 attacks/minute	[511]

C

Supplementary Information for Chapter 4

C.1 Model code

Note: The code for the stochastic model of *in-nido* parasitism was modeled after Aaron King's tutorial: "Exact simulation of birth-death processes via the Gillespie algorithm".

```
Imodel_queen <- function (init , params) {  
  Fs = init[2]  
  Ns = init[3]  
  Bs = init[4]  
  Q = init[5]  
  I = init[6]  
  C = init[7]  
  
  alpha=params["alpha"] # Component of forager transition rate  
  mu=params["mu"] # Natural mortality rate  
  mu_Q=params["mu_Q"] # Queen's natural mortality rate  
  kappa=params["kappa"] # Colony proportion foraging  
  phi=params["phi"] # Brood developmental period  
  lambda=params["lambda"] # Colony birth rate  
  sigma=params["sigma"] # Min. n. ants needed for colony functioning  
  beta=params["beta"] # Force of infection  
  gamma=params["gamma"] # Parasite mortality rate  
  zeta=params["zeta"] # Cadaver decay rate  
  kf=params["kf"] # Forager-Cadaver contact rate  
  kn=params["kn"] # Nest worker-Cadaver contact rate
```

```

kb=params["kf"]          # Brood-Cadaver contact rate
kq=params["kq"]          # Queen-Cadaver contact rate

## each individual rate
rates <- c(
  birth = lambda*(((Fs + Ns + Bs + I)/sigma)^2/(1 + ((Fs + Ns + Bs + I)/sigma)^2)),

  transition_BN = phi*Bs,
  transition_NF = alpha*(kappa - (Fs)/(Fs + Ns + Bs + I + 1))*Ns,

  infection_F = beta*Fs + kf*C*Fs,
  infection_N = kn*C*Ns,
  infection_B = kb*C*Bs,
  infection_Q = kq*C*Q,

  cadaver_generation = gamma*I,
  cadaver_decay = zeta*C,

  Fs_death = mu*Fs,
  Ns_death = mu*Ns,
  Bs_death = mu*Bs,
  Q_death = mu_Q*Q
)

## what changes with each event?
transitions <- list(
  birth=c(0,0,1,0,0,0),

  transition_BN=c(0,1,-1,0,0,0),
  transition_NF=c(1,-1,0,0,0,0),

  infection_F=c(-1,0,0,0,1,0),
  infection_N=c(0,-1,0,0,1,0),
  infection_B=c(0,0,-1,0,1,0),
  infection_Q=c(0,0,0,-1,1,0),

  cadaver_generation=c(0,0,0,0,-1,1),
  cadaver_decay=c(0,0,0,0,0,-1),

  Fs_death=c(-1,0,0,0,0,0),
  Ns_death=c(0,-1,0,0,0,0),

```

```

    Bs_death=c(0,0,-1,0,0,0),
    Q_death=c(0,0,0,-1,0,0)
  )
  ## total event rate
  total.rate <- sum(rates)
  ## waiting time
  if (total.rate==0)
    tau <- Inf
  else
    tau <- rexp(n=1,rate=total.rate)
  ## which event occurs?
  event <- sample.int(n=13,size=1,prob=rates/total.rate)
  init+c(tau,transitions[[event]])
}

Imodel_simul <- function (init , params, maxstep = 50000) {
  output <- array(dim=c(maxstep+1,7))
  colnames(output) <- names(init)
  output[1,] <- init
  k <- 1
  ## loop until either k > maxstep or
  ## there are no more infectives or
  ## Q is dead
  while ((k <= maxstep) && (init["Q"] > 0) &&
  ((init["Fs"] + init["Ns"] + init["Bs"]) > 0)) {
    k <- k+1
    output[k,] <- init <- Imodel_queen(init ,params)
  }
  as.data.frame(output[1:k,])
}

```

D

Supplementary Information for Chapter 5

D.1 Methods

Ant-time calculation

To calculate ant-time, we took the number of ants in each functional group for each night of observation and multiplied by the total time they were in the nest and therefore available to engage in trophallaxis interactions with other ants. The queen, nest workers, and inactive foragers were by definition in the nest for the entire 20-minute observation period each night and accordingly the calculation of ant-time is a simple product of the number of those ants by the 1,210-second observation window. However, foragers were in the nest for variable amounts of time and so ant-time for the forager class is calculated by summing how much time each individual forager was in the nest for a precise calculation of the time they were available for within-nest interactions. The ant-time formulas are given below:

$$T_F = \sum_{F_i}^{F_n} t_i,$$

where t_i is the amount of time forager F_i spent inside the nest.

$$T_{ant} = N_{ant} \times 1210s,$$

where N_{ant} = number of ants in type *ant*.

Ant movement model

In both colonies, the observed residence times in each grid cell and transitions to neighboring cells were used to fit a continuous-time discrete-space random walk model for ant movement behavior and used to calculate a movement or transition rate between cells. We used a continuous-time discrete-space (CTDS) agent-based random walk model [487, 488] to make inference about ant movement behavior. The CTDS framework is notable in that it allows for inference on both directional (e.g., queen avoidance) and location-based (e.g., variable movement rates in different nest chambers) movement mechanisms. Drawing on standard continuous-time Markov chain models (e.g., [487]), if an ant is in cell i at time t , then define the rate of transition from cell i to a neighboring cell j as λ_{ij} . The total rate $\lambda(i)$ at which ants move (transition) out of cell i is the sum of the rates to all neighboring cells: $\lambda_i = \lambda_{ij}$, and when the ant moves, the probability of moving to cell k (instead of to another neighboring cell) is the ratio: λ_{ik}/λ_i .

To model ant movement behavior near the queen, we will model λ_{ij} as a function of a spatial covariate that measures the distance from the queen's most used locations ('Distance From Queen' - DFQ) at each grid cell. To examine local behavior, the DFQ covariate was set to be constant out of the queen's chamber. The DFQ covariate is location-based and will allow us to model differences in movement rates when near or far from the queen. We also considered a directional covariate, a gradient of the DFQ covariate (GDFQ). The GDFQ gradient is a directional vector that points towards the queen, or along the direction of steepest ascent of the DFQ covariate, and the GDFQ covariate will be different for the transition rates to neighboring cells in different directions, thus allowing for directional preference in ant movement. We also consider potential differences in movement behavior between foraging (F) and non-foraging (NF) ants, with $F=1$ for foraging ants and $F=0$ otherwise, and $NF=0$ for foraging ants and $NF=1$ otherwise. We model the movement rate $\lambda_k(i, j)$ of the k -th ant from cell i to cell j as a function of interactions of these covariates and corresponding regression parameters β :

$$\lambda_k(i, j) = \exp F_k \beta_1 + NF_k \beta_2 + (F_k * DFQ_i) \beta_3 + (NF_k * DFQ_i) \beta_4 \\ + (F_k * GDFQ_{ij}) \beta_5 + (NF_k * GDFQ_{ij}) \beta_5 \quad (D.1)$$

Differences in overall movement rates between foragers and non-foragers will be represented by differences in β_1 and β_2 , with positive values corresponding to higher movement rates. Positive values of β_3 correspond to higher movement rates of foraging ants when far from the queen, and decreased movement rates near the queen. Positive values of β_5 correspond to preferential directional movement by foragers away from the queen (in the direction of the increase in the gradient of DFQ). The parameters β_4 and β_6 correspond to the response of non-foraging ants to DFQ and GDFQ, respectively. Hanks et al. (2013) have shown that inference on the parameters in this movement model can be accomplished using a Poisson GLM, which we fit using the 'glm' command in R.

D.2 Supplemental Tables and Figures

Figure D.1: Static trophallaxis networks.

Unweighted, bi-directional trophallaxis networks for all 8 nights for colonies 1 and 2. Individual ants are represented as circles; their x-y coordinates were randomly generated and maintained in all graphs. Lines between circles represent a trophallaxis interaction between those ants; the length and width of the line conveys no additional information.

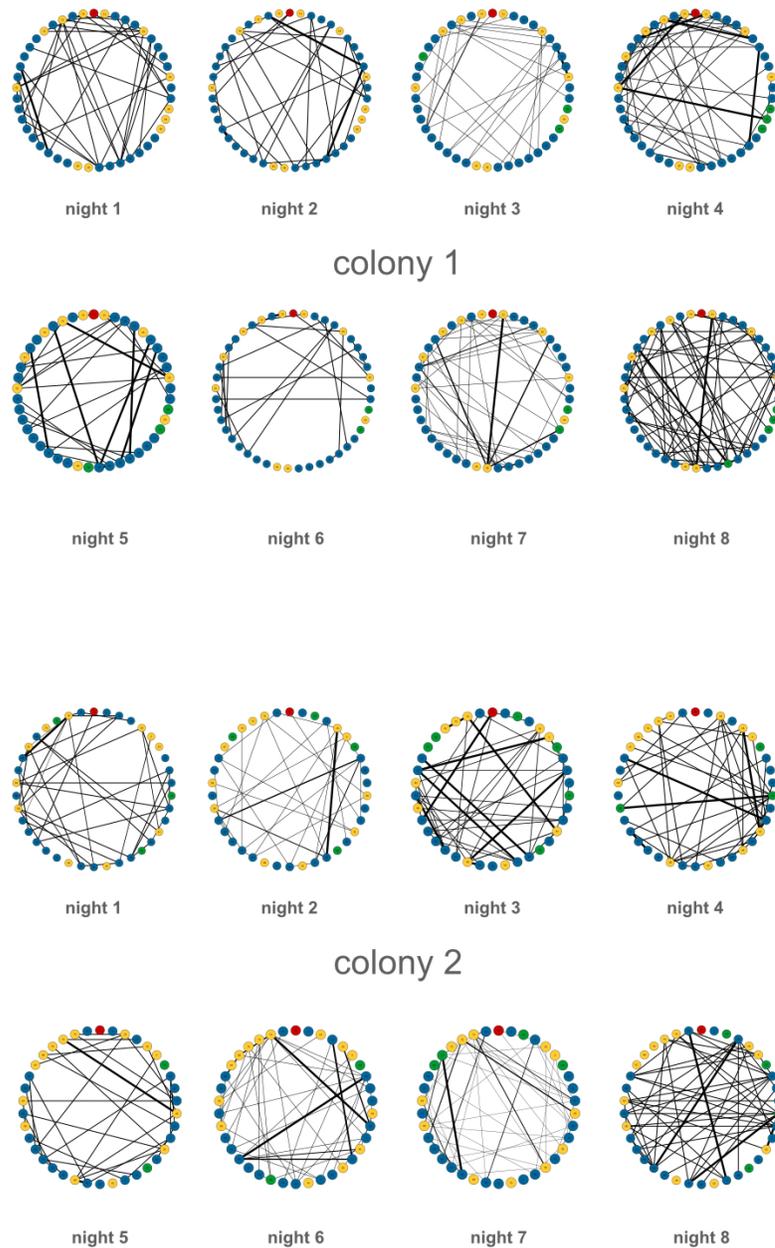
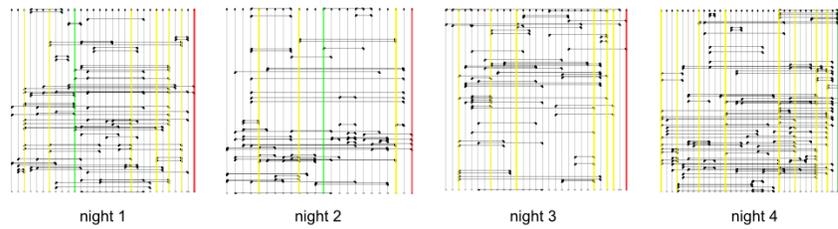
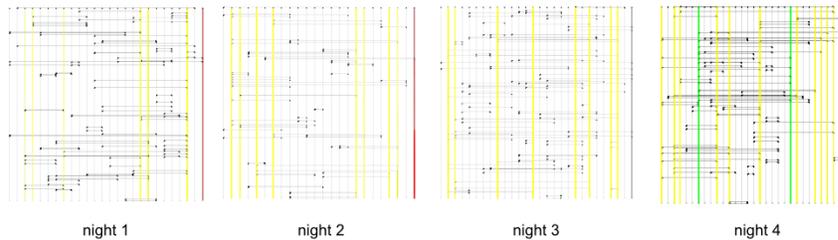
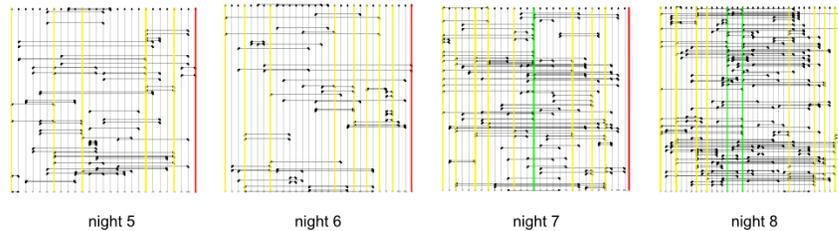


Figure D.2: Time-ordered trophallaxis networks.

Un-weighted, bidirectional, time-ordered networks for all 8 nights for colonies 1 and 2. Individual ants are represented as vertical lines moving through time (time starts at $y = 0$ and moves forward in the $+y$ direction). Horizontal lines represent the start time of trophallaxis interaction between the two individuals connected. Active foragers are shaded in green, inactive foragers are shaded in yellow, nest workers are not shaded, and the queen is shaded in red.



colony 1



colony 2

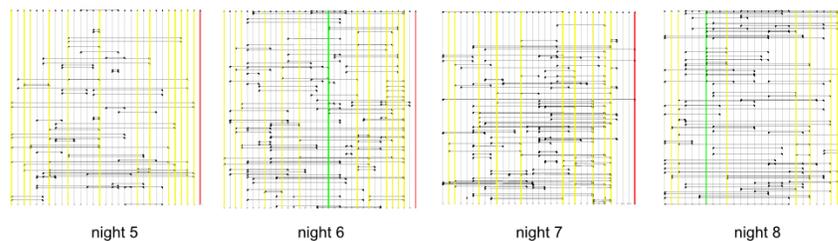


Table D.1: Summaries of selected recent social insect literature.

Summaries of selected recent social insect literature		
Reference	Year	Summary
Naug, D. and Smith, B. Experimentally induced change in infectious period affects transmission dynamics in a social group. <i>Proc. Roy Soc B</i> 274 , 61-65 [476]	2007	Naug and Smith (2007) fed known forager bees on sucrose solutions containing microbeads. They followed the first- and second-order trophallaxis interactions of these foragers and then dissected a random subset of the colony after a pre-determined exposure time to follow microbead transmission. While a realistic and quantitative way to measure the spread of a pathogen proxy, the use of microbeads unfortunately requires destructive sampling. Given the size of the colonies we were working with and because we also wished to investigate individual and functional group networks over time, that requires following whole colony social dynamics over several days, we opted against pursuing microbead transmission in this study. Having characterized whole colony trophallaxis networks with our present study, we are now very keen to explicitly measure microbead transmission in future work.
Otterstatter, M.C. and Thompson, J.D. Contact networks and transmission of an intestinal pathogen in bumble bee (<i>Bombus impatiens</i>) colonies. <i>Oecologia</i> 154 , 411-421 [472]	2007	Otterstatter and Thompson followed the actual transmission of a pathogen through the physical contact network of bumble bee colonies. They investigated transmission through both naturally infected foundresses (vertical transmission) and through infection initiated with infected foragers (horizontal transmission). The major drawback to this study is the small size of the colonies used; numbering between 4-6 workers and a queen. While this may represent a good approximation for disease transmission in founding colonies, it is likely not directly translatable to disease transmission dynamics within larger, established colonies.
Naug, D. Structure of the social network and its influence on the transmission dynamics in a honeybee colony. <i>Behav Ecol Sociobiol</i> 62 , 1719-1725 [475]	2008	Naug (2008) followed the first- and second-order trophallaxis interactions of known forager bees in a single colony. However, while the duration of these trophallaxis events was known, the actual amount of sucrose transferred was not directly measured and duration was used as a proxy. Our study also uses trophallaxis duration as a proxy for quantity transferred, but as addressed below, we cannot infer the directionality as Naug (2008) did. We are currently following up our study to explicitly follow the directed trophallaxis of known foragers once they have returned to the nest and until the entire colony has been reached by time-ordered interactions.

Continuation of Table D.1

Reference	Year	Summary
Buffin, A., <i>et al.</i> Feeding and stocking up: radio-labeled food reveals exchange patterns in ants. <i>PLoS One</i> 4 , e5919 [502]	2009	Buffin <i>et al.</i> (2009) investigated food flow dynamics in ants at the level of the entire colony. Using radioactively labeled food, they followed the rate at which the radiographic signal spread through the colony over time, and where that signal spatially accumulated. While this study provides a great overview at the level of the colony, we don't know how this food flow is accomplished through dyadic-level social interactions, and what the social composition and relative timing of such dyadic interactions was.
Sendova-Franks, A.B. <i>et al.</i> Emergency networking: famine relief in ant colonies. <i>Anim Behav</i> 79 , 473-485 [477]	2010	Sendova-Franks <i>et al.</i> (2010) examined trophallaxis networks in colonies that were maintained in fed followed by semi-starved conditions. They distinguished between internal and external nest workers, and found that increased food flow after semi-starvation was mediated by the spatial movement of internal workers away from brood and movement of foragers deeper into the nest. They also found that under semi-starved conditions, internal workers transitioned from being primarily food receivers to both food receivers and donors, which they suggest could act as a mechanism to dilute potential poisons. Our work follows on this by employing time-ordered network analyses to investigate food flow.
Pinter-Wollman, N. <i>et al.</i> The effect of individual variation on the structure and function of interaction networks in harvester ants. <i>J Roy Soc Interface</i> , rsif20110059 [473]	2011	Pinter-Wollman <i>et al.</i> (2011) looked at information exchange through spatial proximity of ants in the entrance chambers of colonies. From this they found that most ants only had a few interactions and very few ants had the majority of interactions. They also found that the majority of interactions were not randomly distributed but rather occurred in specific hotspots near the chamber entrance. Though this work does a fantastic job of investigating individual differences in spatial interactions, we don't know to what extent this variation also applies to social interactions and to other areas of the nest besides the entrance chamber.
Waters J.M. and Fewell, J.H. Information processing in social insect networks. <i>PLoS One</i> 7 , e40337 [464]	2012	Waters and Fewell (2012) recorded antennation networks for harvester ant colonies and compared the overarching network structure to those of networks from other systems (i.e. technology networks, gene regulatory networks, etc.). They suggest that the network sub-graph motifs they observe may have been selected for as a way to increase information flow. We employ similar motif analyses to look for evidence of social segregation in our present study.

Continuation of Table D.1

Reference	Year	Summary
Jeanson, R. Long-term dynamics in proximity networks in ants. <i>Anim Behav</i> 83 , 915-923 [471]	2012	Jeanson (2012) used RFID tags to follow the spatial movement of individual ants over the course of multiple weeks. From this, they built association networks based upon which ants were near each other. Importantly, this work showed that these spatial proximity networks were stable over time and robust to the removal of the queen. However, whether nest spatial usage correlates to actual social interactions between proximate individuals was not explicitly tested.

End of Table D.1

Table D.2: Statistical test results for trophallaxis count and duration.

(a) Two-sided Kruskal-Wallis tests and (b) Dunn tests differences in trophallaxis count and duration as a function of ant functional classification. Asterisks represent statistically significant differences between groups following a Benjamini-Hochberg correction for multiplicity of hypothesis testing.

	Colony 1		Colony 2	
	χ^2	p-value	χ^2	p-value
Count	20.3349	0.0001447	7.282	0.06343
Duration	6.4096	0.0933	4.386	0.2227
Comparison	z-statistic	p-value	z-statistic	p-value
Forager - Inactive forager	-0.197696	0.4216	-	-
Forager - Nest worker	-1.802277	0.0429	-	-
Forager - Queen	-2.920887	0.0035*	-	-
Inactive forager - Nest worker	-3.420299	0.0019*	-	-
Inactive forager - Queen	-3.324025	0.0013*	-	-
Nest worker - Queen	-2.233482	0.0191*	-	-

Table D.3: Network metrics by ant behavioral class.

(a) Mean static network metrics (degree, betweenness, closeness, and constraint) for each ant functional group and (b) Kruskal-Wallis test results. Network metrics were not weighted by the duration of trophallaxis, only trophallaxis count.

a. Mean network metrics by ant functional class				
Colony 1				
	Forager	Inactive	Nest	Queen
Degree centrality	5.4444	4.2115	3.3005	1.8
Betweenness centrality	34.77253856	30.5094339	21.61129782	8.4
Closeness centrality	0.008250487	0.006071785	0.008876807	0.003385343
Burt's constraint	0.553180156	0.507645737	0.604037759	0.9
Colony 2				
Degree centrality	6	3.636	2.454	2
Betweenness centrality	61.0345	29.826	23.9633	15.01786
Closeness centrality	0.008805486	0.010156424	0.008386321	0.010619818
Burt's constraint	0.3614429	0.546924036	0.540063961	0.687029325
b. Kruskal-Wallis test on network metrics				
	Colony 1		Colony 2	
	χ^2	p-value	χ^2	p-value
Degree centrality	25.0686	0.00001494	19.9183	0.0001765
Betweenness centrality	14.9998	0.001817	8.3246	0.03976
Closeness centrality	15.164	0.001682	3.868	0.2761
Burt's constraint	11.1124	0.01113	3.7467	0.2901

Table D.4: Statistical test results for network metrics by ant behavioral class.

Dunn tests results for differences in mean static network metrics (degree, betweenness, closeness, and constraint) for each ant functional group. Asterisks represent statistically significant differences between groups following a Benjamini-Hochberg correction for multiplicity of hypothesis testing. Network metrics were not weighted by the duration of trophallaxis, only trophallaxis count.

Post-hoc Dunn test results				
	Colony 1		Colony 2	
	z-statistic	p-value	z-statistic	p-value
Degree centrality				
Forager - Inactive	-0.474675	0.3175	-1.441133	0.1122
Forager - Nest	-2.514156	0.0179*	-2.491783	0.0191*
Forager - Queen	-2.005933	0.0336	-1.980356	0.0477
Inactive - Nest	-4.432227	0.0000*	-3.836072	0.0004*
Inactive - Queen	-2.023584	0.043	-1.289485	0.1183
Nest - Queen	-0.583159	0.3359	-0.279067	0.3901
Betweenness centrality				
Forager - Inactive	-0.070616	0.4719	-1.17404	0.1442
Forager - Nest	-1.612799	0.0801	-1.77347	0.0762
Forager - Queen	-1.849027	0.0645	-1.852814	0.0959
Inactive - Nest	3.390584	0.0021*	-2.169286	0.0902
Inactive - Queen	-2.148224	0.0475	-1.380717	0.1255
Nest - Queen	-1.067462	0.1715	-0.818929	0.2064
Closeness centrality				
Forager - Inactive	-1.461944	0.0863	-	-
Forager - Nest	-2.788372	0.0159*	-	-
Forager - Queen	-2.381952	0.0172*	-	-
Inactive - Nest	-2.726254	0.0096*	-	-
Inactive - Queen	-1.710273	0.0654	-	-
Nest - Queen	-0.840669	0.2003	-	-
Burt's constraint				
Forager - Inactive	0.028268	0.4887	-	-
Forager - Nest	1.118676	0.158	-	-
Forager - Queen	2.287563	0.0222*	-	-
Inactive - Nest	2.355095	0.0278*	-	-
Inactive - Queen	2.703288	0.0206*	-	-
Nest - Queen	1.969885	0.0366	-	-

Table D.5: Percentage of time budget engaged in trophallaxis.

Mean and standard deviation of percentage time budget engaged in trophallaxis for each functional group comparison. The functional group on the left-most side in each label is the focal group, and it is their ant-time used in the denominator.

Mean percent time budget engaged in trophallaxis				
	Colony 1		Colony 2	
	z-statistic	p-value	z-statistic	p-value
Forager - Forager	0.131	-	4.797	-
Forager - Inactive	0.372	0.283	9.956	5.295
Forager - Nest	0.301	0.296	10.5	7.067
Forager - Queen	-	-	-	-
Inactive - Inactive	0.914	1.829	1.702	1.014
Inactive - Forager	1.237	1.168	0.616	0.385
Inactive - Nest	0.912	0.516	4.054	2.924
Inactive - Queen	-	-	-	-
Nest - Nest	2.534	0.988	3.197	0.992
Nest - Active	0.529	0.408	0.35	0.113
Nest - Inactive	1.171	0.698	2.077	1.65
Nest - Queen	0.138	0.134	0.199	0.174
Queen - Active	-	-	-	-
Queen - Inactive	-	-	-	-
Queen - Nest	5.5	5.091	4.173	3.587

Table D.6: Inference on ant movement parameters.

Inference on ant movement parameters in a continuous-time random walk model of ant movement in two ant colonies (See Figure 5.4).

	Effect	Estimate	Std. Error	p-value (T-test)
Colony 1	F	-3.18845	0.04111	$<10^{-15}$
	NF	-1.63299	0.03379	$<10^{-15}$
	F*DFQ	-0.04696	0.04114	0.25371
	NF*DFQ	0.12605	0.03304	0.00014
	F*GDFQ	-0.02391	0.0412	0.5616
	NF*GDFQ	-0.0077	0.03221	0.081119
Colony 2	F	-2.2599	0.02222	$<10^{-15}$
	NF	-0.92576	0.02035	$<10^{-15}$
	F*DFQ	-0.19091	0.02453	$<10^{-14}$
	NF*DFQ	0.04115	0.01435	0.00416
	F*GDFQ	-0.01581	0.03571	0.65801
	NF*GDFQ	-0.00106	0.01023	0.91763

APPENDIX E

E

Supplementary Information for Chapter 6

Please refer to Chapter 6 for complete results and discussion. Here we provide the static network metrics for the ant trophallaxis networks and additional figures for the simulated resource spread analyses.

E.1 Supplemental Tables and Figures

Table E.1: Static network metrics.

Mean static network metrics (degree, betweenness) by ant type for colonies 1-3.

Mean static network metrics.						
	Colony 1		Colony 2		Colony 3	
	Degree	Betweenness	Degree	Betweenness	Degree	Betweenness
Forager	38.6	42.90533	27.25	30.77727	16	50.64495
Nest	17.80556	53.46505	14.80556	77.37595	18.4	64.39171
Retinue	16.125	61.36185	13.125	109.0482	27.25	105.7148
Queen	24	126.1024	8	85.44935	30	55.62425

Table E.2: Statistical results for static network metrics.

Kruskal-Wallis χ^2 , degrees of freedom, and p-values for differences in degree and betweenness by ant type. Asterisks represent statistically significant differences between groups at $\alpha = 0.05$ level.

Kruskal-Wallis results			
Static network degree centrality			
	χ^2	df	<i>p-value</i>
Colony 1	6.6854	3	0.08
Colony 2	6.3957	3	0.09
Colony 3	11.7235	3	0.01*
Static network betweenness centrality			
Colony 1	5.3935	3	0.15
Colony 2	2.0489	3	0.56
Colony 3	14.0757	3	0.003*
Significant Dunn test results			
	Metric	Group comparison	<i>p-value</i>
Colony 3	Degree	Nest worker - Retinue	0.0031*
Colony 3	Betweenness	Nest worker - Retinue	.0007*

Figure E.1: Static network metrics.

Static network metrics (degree and betweenness centrality) as a function of ant behavioral group for colonies 1- 3. Solid black lines represent the median values, boxes represent data within the 25th - 75th percentiles, and whiskers extend to 1.5 times the interquartile range. Asterisks represent statistically significant differences between groups using Kruskal-Wallis tests

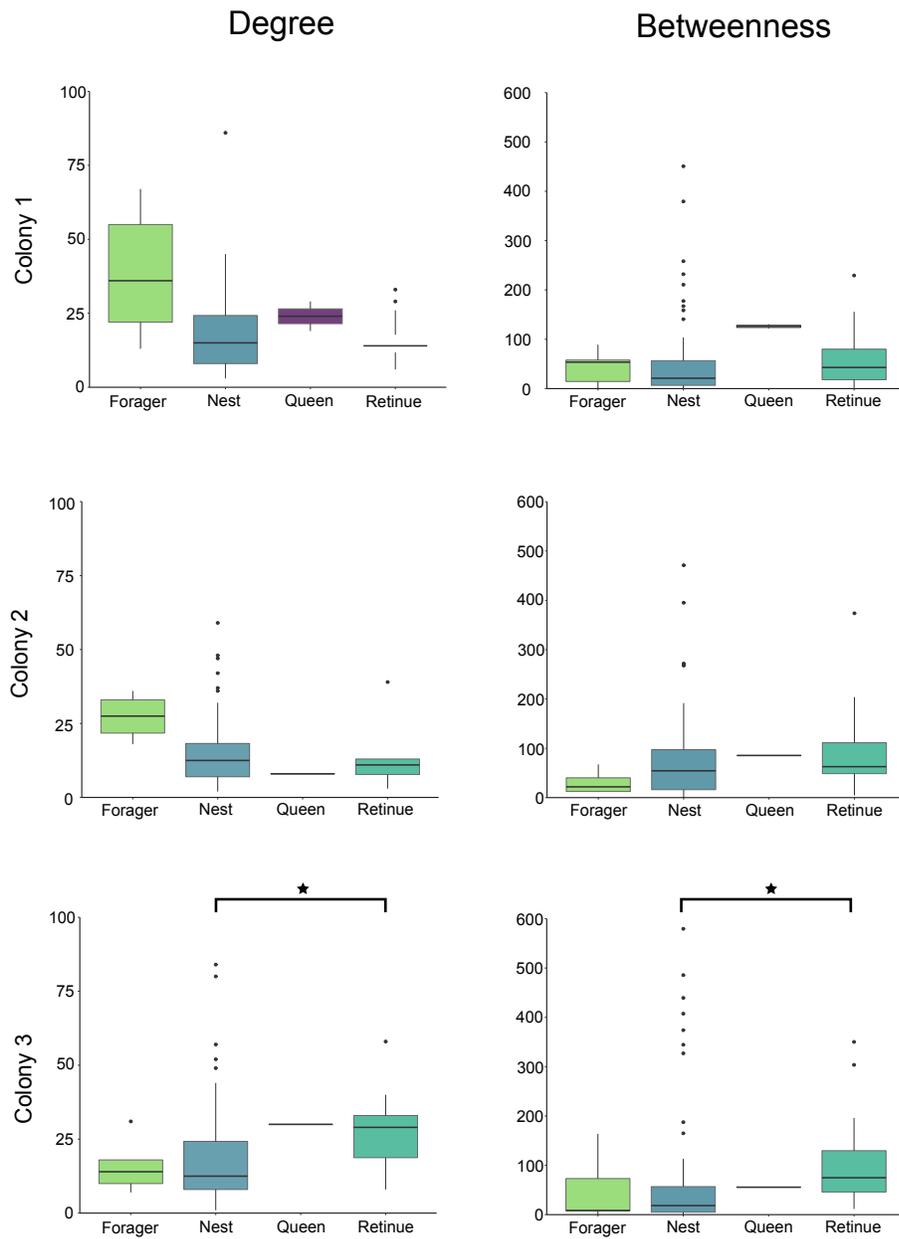


Figure E.2: Time to 10% colony saturation as a function of ant type.

Violin plots showing the distributions of minimum time needed to reach 10% colony saturation with food as a function of the food decay period and ant type for all colonies combined together.

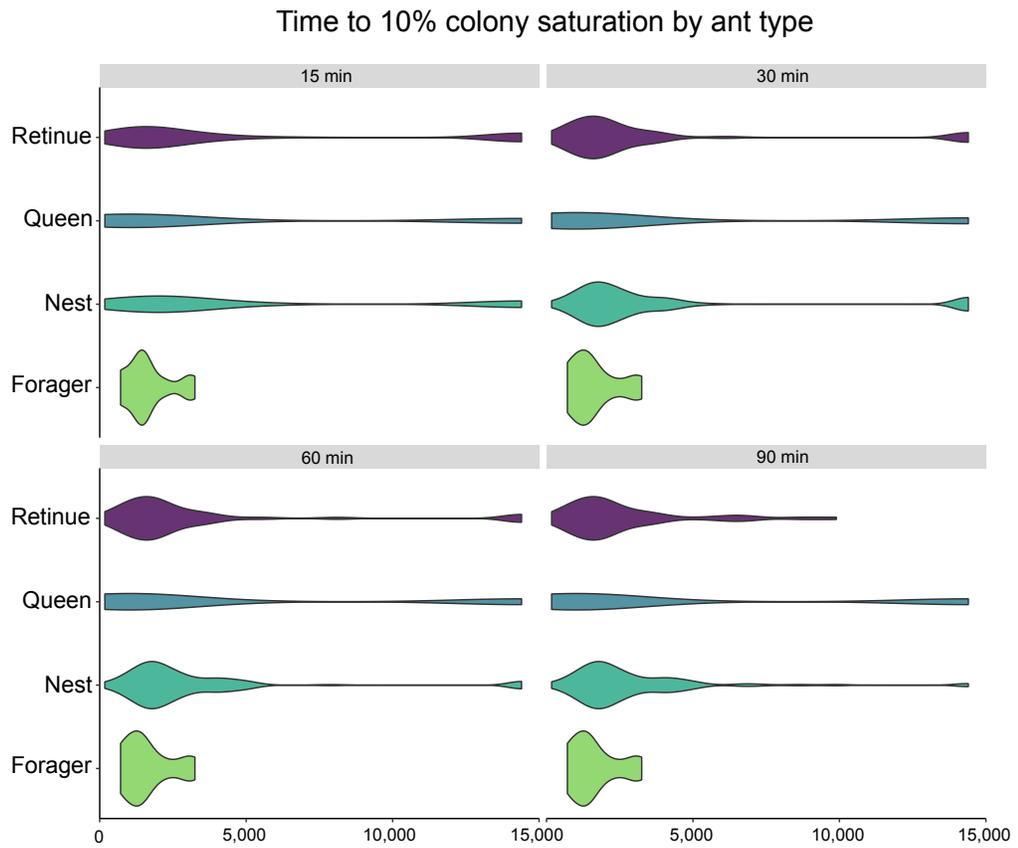


Figure E.3: Time to 25% colony saturation as a function of ant type.

Violin plots showing the distributions of minimum time needed to reach 25% colony saturation with food as a function of the food decay period and ant type for all colonies combined together.

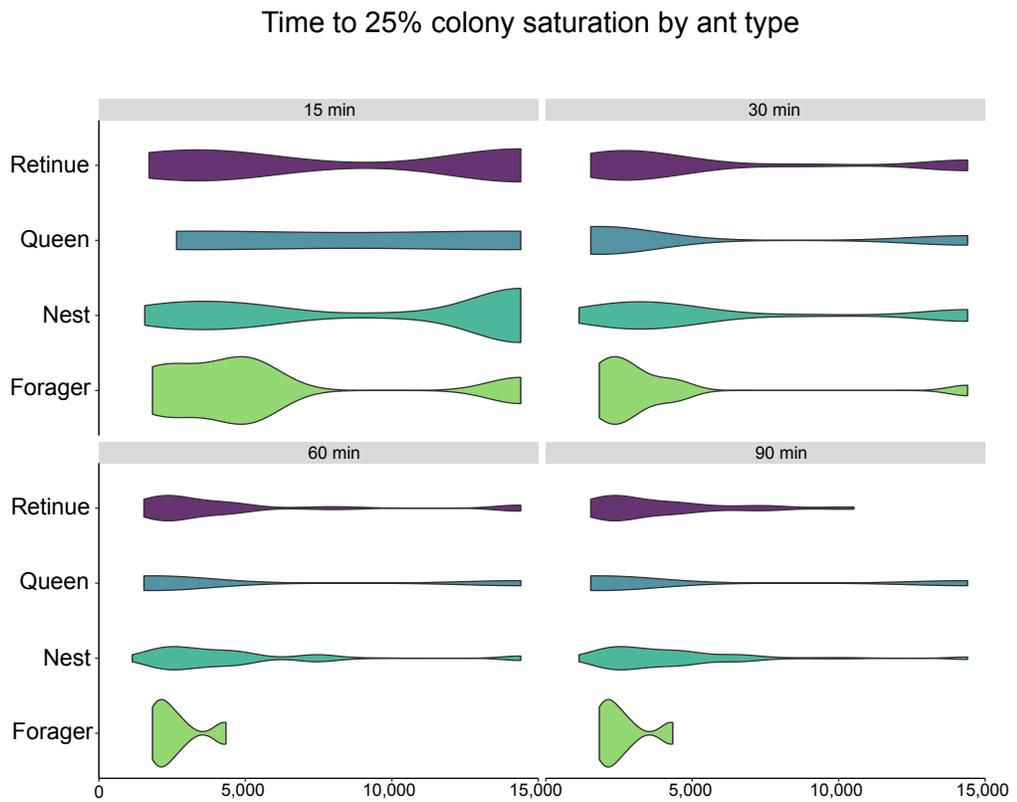


Figure E.4: Time to 50% colony saturation as a function of ant type.

Violin plots showing the distributions of minimum time needed to reach 50% colony saturation with food as a function of the food decay period and ant type for all colonies combined together.

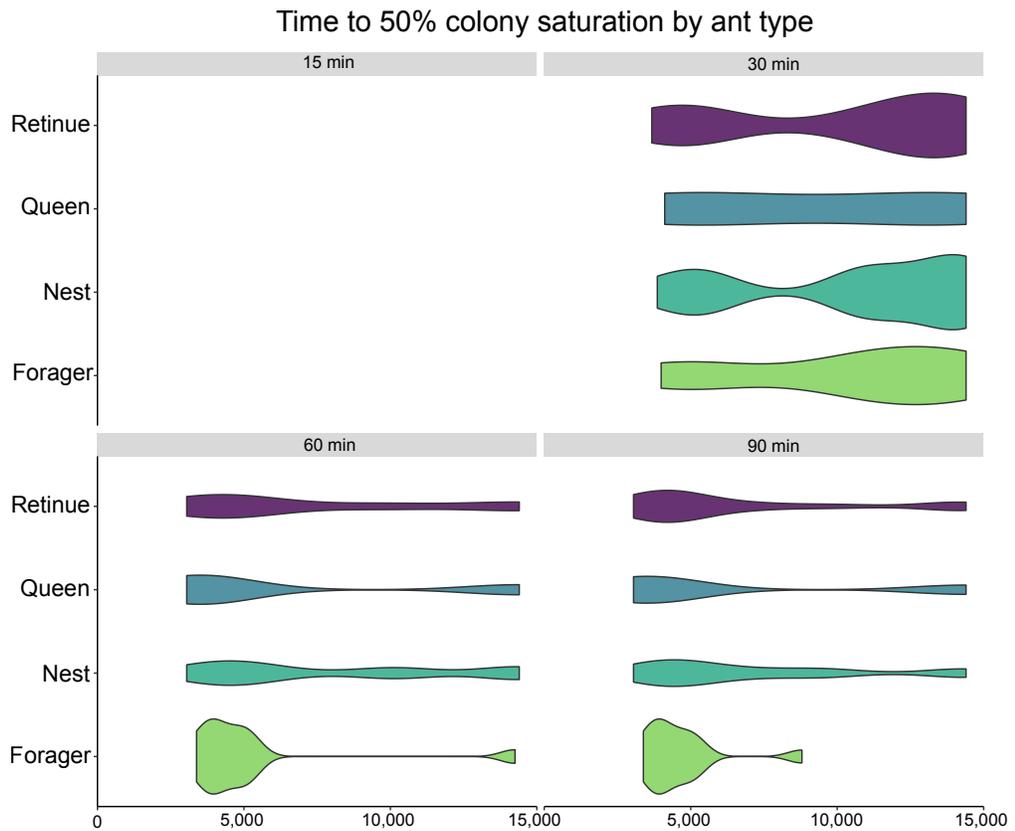
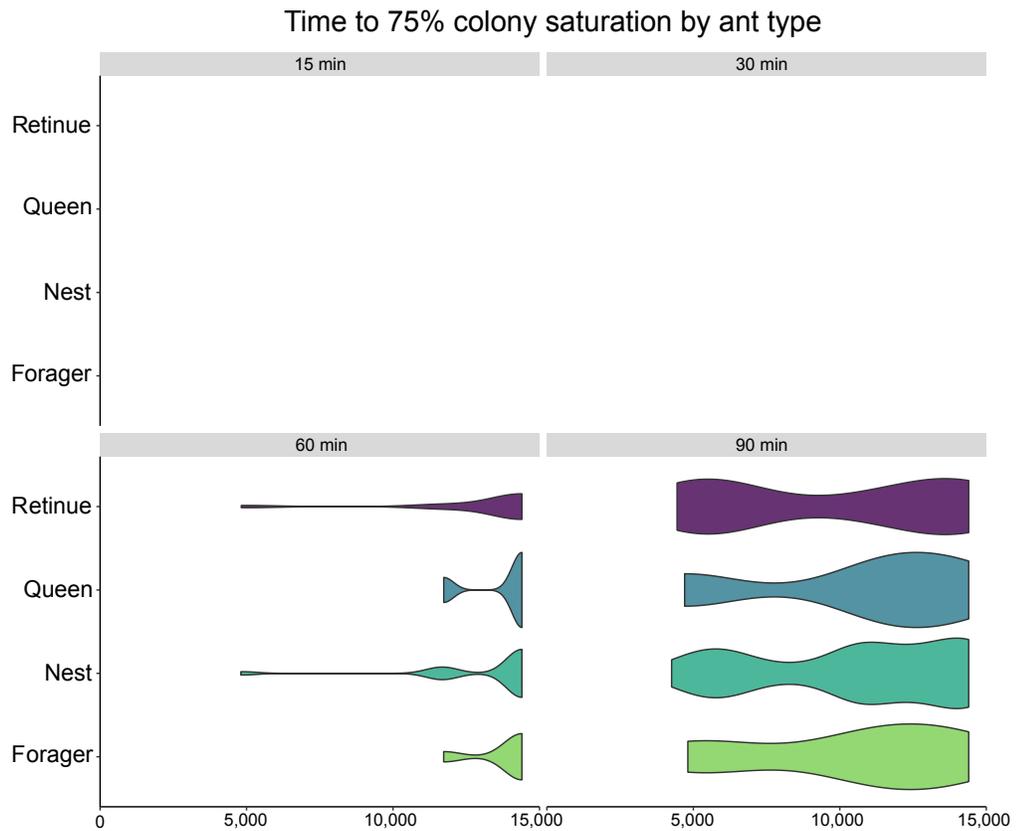


Figure E.5: Time to 75% colony saturation as a function of ant type.

Violin plots showing the distributions of minimum time needed to reach 75% colony saturation with food as a function of the food decay period and ant type for all colonies combined together.



Bibliography

- [1] ARNEBERG, P., A. SKORPING, B. GRENFELL, and A. F. READ (1998) "Host densities as determinants of abundance in parasite communities," *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **265**(1403), pp. 1283–1289.
- [2] CÔTÉ, I. M. and R. B. POULIN (1995) "Parasitism and group size in social animals: a meta-analysis," *Behavioral Ecology*, **6**(2), pp. 159–165.
- [3] ALTIZER, S., C. L. NUNN, P. H. THRALL, J. L. GITTLEMAN, J. ANTONOVICS, A. A. CUNNINGHAM, A. P. DOBSON, V. EZENWA, and K. E. JONES (2003) "Social organization and parasite risk in mammals: integrating theory and empirical studies," *Annual Review of Ecology, Evolution, and Systematics*, **34**, pp. 517–547.
- [4] MOREAU, C. S., C. D. BELL, R. VILA, S. B. ARCHIBALD, and N. E. PIERCE (2006) "Phylogeny of the ants: diversification in the age of angiosperms," *Science*, **312**(5770), pp. 101–104.
- [5] HÖLLDOBLER, B. and E. O. WILSON (1990) *The Ants*, Harvard University Press.
- [6] SCHULTZ, T. R. (2000) "In search of ant ancestors," *Proceedings of the National Academy of Sciences*, **97**(26), pp. 14028–14029.
- [7] BOLTON, B. (2018), "AntCat: An online catalog of the ants of the world," .
- [8] BECK, L. (1971) "Bodenzoologische Gliederung und Charakterisierung des amazonischen Regenwaldes," *Amazonia Limnol Oecol Reg Syst Fluminis Amazonas*.
- [9] FITTKAU, E. J. and H. KLINGE (1973) "On biomass and trophic structure of the central Amazonian rain forest ecosystem," *Biotropica*, pp. 2–14.
- [10] TOBIN, J. E. (1995) "Ecology and diversity of tropical forest canopy ants," *Forest Canopies*, pp. 129–147.
- [11] DAVIDSON, D. W. (1997) "The role of resource imbalances in the evolutionary ecology of tropical arboreal ants," *Biological Journal of the Linnean Society*, **61**(2), pp. 153–181.

- [12] WILSON, E. O. and R. W. TAYLOR (1967) "An estimate of the potential evolutionary increase in species density in the Polynesian ant fauna," *Evolution*, **21**(1), pp. 1–10.
- [13] FOLGARAIT, P. J. (1998) "Ant biodiversity and its relationship to ecosystem functioning: a review," *Biodiversity & Conservation*, **7**(9), pp. 1221–1244.
- [14] MENKE, S. B., W. BOOTH, R. R. DUNN, C. SCHAL, E. L. VARGO, and J. SILVERMAN (2010) "Is it easy to be urban? Convergent success in urban habitats among lineages of a widespread native ant," *PLoS One*, **5**(2), p. e9194.
- [15] SCHNEIRLA, T. (1971) *Army ants: a study in social organization*.
- [16] BRADY, S. G., B. L. FISHER, T. R. SCHULTZ, and P. S. WARD (2014) "The rise of army ants and their relatives: diversification of specialized predatory doryline ants," *BMC Evolutionary Biology*, **14**(1), p. 93.
- [17] MUELLER, U. G., S. A. REHNER, and T. R. SCHULTZ (1998) "The evolution of agriculture in ants," *Science*, **281**(5385), pp. 2034–2038.
- [18] MUELLER, U. G., N. M. GERARDO, D. K. AANEN, D. L. SIX, and T. R. SCHULTZ (2005) "The evolution of agriculture in insects," *Annual Review of Ecology, Evolution, and Systematics*, **36**, pp. 563–595.
- [19] RUSSELL, J. A., C. S. MOREAU, B. GOLDMAN-HUERTAS, M. FUJIWARA, D. J. LOHMAN, and N. E. PIERCE (2009) "Bacterial gut symbionts are tightly linked with the evolution of herbivory in ants," *Proceedings of the National Academy of Sciences*, **106**(50), pp. 21236–21241.
- [20] STYRSKY, J. D. and M. D. EUBANKS (2007) "Ecological consequences of interactions between ants and honeydew-producing insects," *Proceedings of the Royal Society of London B: Biological Sciences*, **274**(1607), pp. 151–164.
- [21] CURRIE, C. R. and A. E. STUART (2001) "Weeding and grooming of pathogens in agriculture by ants," *Proceedings of the Royal Society of London B: Biological Sciences*, **268**(1471), pp. 1033–1039.
- [22] KISTNER, D. H. (1982) *The Social Insects' Bestiary*, vol. 3, chap. The Social Insects' Bestiary, Academic Press, pp. 1–244.
- [23] HEIL, M. and D. MCKEY (2003) "Protective ant-plant interactions as model systems in ecological and evolutionary research," *Annual Review of Ecology, Evolution, and Systematics*, **34**(1), pp. 425–553.
- [24] HAINES, B. (1978) "Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica*, in Panama," *Biotropica*, pp. 270–277.

- [25] HOWE, H. F. and J. SMALLWOOD (1982) "Ecology of seed dispersal," *Annual Review of Ecology and Systematics*, **13**(1), pp. 201–228.
- [26] ALLEN, C. R., S. DEMARAIS, and R. S. LUTZ (1994) "Red imported fire ant impact on wildlife: an overview," *The Texas Journal of Science*, **46**.
- [27] ALLEN, C. R., R. S. LUTZ, and S. DEMARAIS (1995) "Red imported fire ant impacts on northern bobwhite populations," *Ecological Applications*, **5**(3), pp. 632–638.
- [28] JOHNSON, B. R., M. L. BOROWIEC, J. C. CHIU, E. K. LEE, J. ATALLAH, and P. S. WARD (2013) "Phylogenomics resolves evolutionary relationships among ants, bees, and wasps," *Current Biology*, **23**(20), pp. 2058–2062.
- [29] BRANSTETTER, M. G., B. N. DANFORTH, J. P. PITTS, B. C. FAIRCLOTH, P. S. WARD, M. L. BUFFINGTON, M. W. GATES, R. R. KULA, and S. G. BRADY (2017) "Phylogenomic insights into the evolution of stinging wasps and the origins of ants and bees," *Current Biology*, **27**(7), pp. 1019–1025.
- [30] MOREAU, C. S. and C. D. BELL (2013) "Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants," *Evolution*, **67**(8), pp. 2240–2257.
- [31] SZATHMÁRY, E. and J. M. SMITH (1995) "The major evolutionary transitions," *Nature*, **374**(6519), pp. 227–232.
- [32] CAMERON, S. A. (1993) "Multiple origins of advanced eusociality in bees inferred from mitochondrial DNA sequences," *Proceedings of the National Academy of Sciences*, **90**(18), pp. 8687–8691.
- [33] DUFFY, J. E., C. L. MORRISON, and R. R. ÍOS (2000) "Multiple origins of eusociality among sponge-dwelling shrimps (*Synalpheus*)," *Evolution*, **54**(2), pp. 503–516.
- [34] CHAPMAN, T., B. CRESPI, B. KRANZ, and M. SCHWARZ (2000) "High relatedness and inbreeding at the origin of eusociality in gall-inducing thrips," *Proceedings of the National Academy of Sciences*, **97**(4), pp. 1648–1650.
- [35] DANFORTH, B. N. (2002) "Evolution of sociality in a primitively eusocial lineage of bees," *Proceedings of the National Academy of Sciences*, **99**(1), pp. 286–290.
- [36] BRADY, S. G., S. SIPES, A. PEARSON, and B. N. DANFORTH (2006) "Recent and simultaneous origins of eusociality in halictid bees," *Proceedings of the Royal Society of London B: Biological Sciences*, **273**(1594), pp. 1643–1649.
- [37] INWARD, D., G. BECCALONI, and P. EGGLETON (2007) "Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches," *Biology Letters*, **3**(3), pp. 331–335.

- [38] WILSON, E. O. (1971) *The Insect Societies*, Belknap Press.
- [39] ——— (1975) *Sociobiology*, Belknap/Harvard University Press, Cambridge, MA.
- [40] EVANS, H. E. “The evolution of social life in wasps,” *Proceedings of the 10th International Congress of Entomology*, **2**, pp. 449–457.
- [41] MICHENER, C. D. (1985) “From solitary to eusocial: need there be a series of intervening species?” .
- [42] REHAN, S. M. and A. L. TOTH (2015) “Climbing the social ladder: the molecular evolution of sociality,” *Trends in ecology & evolution*, **30**(7), pp. 426–433.
- [43] MICHENER, C. D. (1969) “Comparative social behavior of bees,” *Annual Review of Entomology*, **14**(1), pp. 299–342.
- [44] HAMILTON, W. D. (1964) “The genetical evolution of social behaviour. II,” *Journal of Theoretical Biology*, **7**(1), pp. 17–52.
- [45] QUELLER, D. C. and J. E. STRASSMANN (1998) “Kin selection and social insects,” *Bioscience*, **48**(3), pp. 165–175.
- [46] FRANK, S. A. (1998) *Foundations of Social Evolution*, Princeton University Press.
- [47] HUGHES, D. P., N. E. PIERCE, and J. J. BOOMSMA (2008) “Social insect symbionts: evolution in homeostatic fortresses,” *Trends in Ecology & Evolution*, **23**(12), pp. 672–677.
- [48] WILSON, E. O. and B. HÖLLDOBLER (2005) “Eusociality: origin and consequences,” *Proceedings of the National Academy of Sciences*, **102**(38), pp. 13367–13371.
- [49] MACEVICZ, S. and G. OSTER (1976) “Modeling social insect populations II: optimal reproductive strategies in annual eusocial insect colonies,” *Behavioral Ecology and Sociobiology*, **1**(3), pp. 265–282.
- [50] BOURKE, A. F. and N. R. FRANKS (1995) *Social Evolution in Ants*, Princeton University Press.
- [51] ROBINSON, G. E., R. E. PAGE JR, and Z.-Y. HUANG (1994) “Temporal polyethism in social insects is a developmental process,” *Animal Behaviour*, **48**(2), pp. 467–469.
- [52] THERAULAZ, G., E. BONABEAU, and J. DENUEBOURG (1998) “Response threshold reinforcements and division of labour in insect societies,” *Proceedings of the Royal Society of London B: Biological Sciences*, **265**(1393), pp. 327–332.

- [53] PINTER-WOLLMAN, N. (2012) "Personality in social insects: how does worker personality determine colony personality?" *Current Zoology*, **58**(4), pp. 580–588.
- [54] CHARBONNEAU, D. and A. DORNHAUS (2015) "When doing nothing is something. How task allocation strategies compromise between flexibility, efficiency, and inactive agents," *Journal of Bioeconomics*, **17**(3), pp. 217–242.
- [55] SCHNEIRLA, T. C. (1953) "Modifiability in insect behavior," *Insect Physiology*, pp. 23–747.
- [56] ROSENGREN, R. (1971) "Route fidelity, visual memory and recruitment behaviour in foraging wood ants of the genus *Formica*: (Hymenoptera, Formicidae)," *Societas Pro Fauna et Flora Fennica*.
- [57] CHITTKA, L. and H. MULLER (2009) "Learning, specialization, efficiency and task allocation in social insects," *Communicative & Integrative Biology*, **2**(2), pp. 151–154.
- [58] OSTER, G. F. and E. O. WILSON (1978) *Caste and Ecology in the Social Insects*, Princeton University Press.
- [59] WILSON, E. O. (1983) "Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*)," *Behavioral Ecology and Sociobiology*, **14**(1), pp. 47–54.
- [60] UGELVIG, L. V., D. J. KRONAUER, A. SCHREMPE, J. HEINZE, and S. CREMER (2010) "Rapid anti-pathogen response in ant societies relies on high genetic diversity," *Proceedings of the Royal Society of London B: Biological Sciences*, **277**(1695), pp. 2821–2828.
- [61] HÖLLDOBLER, B. and E. O. WILSON (2009) *The Superorganism: the Beauty, Elegance, and Strangeness of Insect Societies*, WW Norton & Company.
- [62] GORDON, D. M. (2002) "The organization of work in social insect colonies," *Complexity*, **8**(1), pp. 43–46.
- [63] DENEUBOURG, J.-L. and S. GOSS (1989) "Collective patterns and decision-making," *Ethology, Ecology & Evolution*, **1**(4), pp. 295–311.
- [64] PAGE JR, R. E. and S. D. MITCHELL (1998) "Self-organization and the evolution of division of labor," *Apidologie*, **29**(1-2), pp. 171–190.
- [65] GORDON, D. M. (1992) "Nest relocation in harvester ants," *Annals of the Entomological Society of America*, **85**(1), pp. 44–47.
- [66] BONABEAU, E. (1998) "Social insect colonies as complex adaptive systems," *Ecosystems*, **1**(5), pp. 437–443.

- [67] THERAULAZ, G., E. BONABEAU, S. C. NICOLIS, R. V. SOLÉ, V. FOURCASSIÉ, S. BLANCO, R. FOURNIER, J.-L. JOLY, P. FERNÁNDEZ, and A. GRIMAL (2002) “Spatial patterns in ant colonies,” *Proceedings of the National Academy of Sciences*, **99**(15), pp. 9645–9649.
- [68] GORDON, D. M. (2007) “Control without hierarchy,” *Nature*, **446**(7132), p. 143.
- [69] MIKHEYEV, A. and W. TSCHINKEL (2004) “Nest architecture of the ant *Formica pallidefulva*: structure, costs and rules of excavation,” *Insectes Sociaux*, **51**(1), pp. 30–36.
- [70] DENEUBOURG, J.-L., S. ARON, S. GOSS, and J. M. PASTEELS (1990) “The self-organizing exploratory pattern of the argentine ant,” *Journal of Insect Behavior*, **3**(2), pp. 159–168.
- [71] ROBSON, S. K. and J. F. TRANIELLO (1998) “Resource assessment, recruitment behavior, and organization of cooperative prey retrieval in the ant *Formica schaufussi* (Hymenoptera: Formicidae),” *Journal of Insect Behavior*, **11**(1), pp. 1–22.
- [72] REID, C. R., M. J. LUTZ, S. POWELL, A. B. KAO, I. D. COUZIN, and S. GARNIER (2015) “Army ants dynamically adjust living bridges in response to a cost-benefit trade-off,” *Proceedings of the National Academy of Sciences*, **112**(49), pp. 15113–15118.
- [73] ALEXANDER, R. D. (1974) “The evolution of social behavior,” *Annual Review of Ecology and Systematics*, **5**, pp. 325–383.
- [74] FREELAND, W. (1976) “Pathogens and the evolution of primate sociality,” *Biotropica*, **8**(1), pp. 12–24.
- [75] HOOGLAND, J. L. (1979) “Aggression, ectoparasitism, and other possible costs of prairie dog (*Sciuridae*, *Cynomys spp.*) coloniality,” *Behaviour*, **69**(1), pp. 1–34.
- [76] BROWN, C. R. and M. B. BROWN (1986) “Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*),” *Ecology*, **67**(5), pp. 1206–1218.
- [77] MØLLER, A. P., R. DUFVA, and K. ALLANDER (1993) “Parasites and the evolution of host social behavior,” *Advances in the Study of Behavior*, **22**(65102), pp. 60405–2.
- [78] KRAUSE, J. and G. D. RUXTON (2002) *Living in Groups*, Oxford University Press.
- [79] PATTERSON, J. E. and K. E. RUCKSTUHL (2013) “Parasite infection and host group size: a meta-analytical review,” *Parasitology*, **140**(7), pp. 803–813.

- [80] SCHMID-HEMPEL, P. (2017) “Parasites and their social hosts,” *Trends in Parasitology*, **33**(6), pp. 453–462.
- [81] HAN, B. A., A. W. PARK, A. E. JOLLES, and S. ALTIZER (2015) “Infectious disease transmission and behavioural allometry in wild mammals,” *Journal of Animal Ecology*, **84**(3), pp. 637–646.
- [82] ALTIZER, S., R. BARTEL, and B. A. HAN (2011) “Animal migration and infectious disease risk,” *Science*, **331**(6015), pp. 296–302.
- [83] HALL, R. J., S. ALTIZER, and R. A. BARTEL (2014) “Greater migratory propensity in hosts lowers pathogen transmission and impacts,” *Journal of Animal Ecology*, **83**(5), pp. 1068–1077.
- [84] SATTERFIELD, D. A., J. C. MAERZ, and S. ALTIZER (2015) “Loss of migratory behaviour increases infection risk for a butterfly host,” *Proceedings of the Royal Society of London B: Biological Sciences*, **282**(1801).
- [85] EZENWA, V. O. (2004) “Host social behavior and parasitic infection: a multifactorial approach,” *Behavioral Ecology*, **15**(3), pp. 446–454.
- [86] RIFKIN, J. L., C. L. NUNN, and L. Z. GARAMSZEGI (2012) “Do animals living in larger groups experience greater parasitism? A meta-analysis,” *The American Naturalist*, **180**(1), pp. 70–82.
- [87] NUNN, C. L., F. JORDÁN, C. M. MCCABE, J. L. VERDOLIN, and J. H. FEWELL (2015) “Infectious disease and group size: more than just a numbers game,” *Philosophical Transactions of the Royal Society B: Biological Sciences*, **370**(1669).
- [88] BOURKE, A. (1999) “Colony size, social complexity and reproductive conflict in social insects,” *Journal of Evolutionary Biology*, **12**(2), pp. 245–257.
- [89] BURCHILL, A. and C. MOREAU (2016) “Colony size evolution in ants: macroevolutionary trends,” *Insectes Sociaux*, **63**(2), pp. 291–298.
- [90] LUCKY, A., M. D. TRAUTWEIN, B. S. GUENARD, M. D. WEISER, and R. R. DUNN (2013) “Tracing the rise of ants-out of the ground,” *PloS One*, **8**(12), p. e84012.
- [91] SCHMID-HEMPEL, P. (1998) *Parasites in Social Insects*, Princeton University Press.
- [92] MEUNIER, J. (2015) “Social immunity and the evolution of group living in insects,” *Philosophical Transactions of the Royal Society B: Biological Sciences*, **370**(1669).

- [93] WILSON, K., R. KNELL, M. BOOTS, and J. KOCH-OSBORNE (2003) "Group living and investment in immune defence: an interspecific analysis," *Journal of Animal Ecology*, **72**(1), pp. 133–143.
- [94] ALMBERG, E. S., P. C. CROSS, A. P. DOBSON, D. W. SMITH, M. C. METZ, D. R. STAHLER, and P. J. HUDSON (2015) "Social living mitigates the costs of a chronic illness in a cooperative carnivore," *Ecology Letters*, **18**(7), pp. 660–667.
- [95] EZENWA, V. O., E. A. ARCHIE, M. E. CRAFT, D. M. HAWLEY, L. B. MARTIN, J. MOORE, and L. WHITE (2016) "Host behaviour–parasite feedback: an essential link between animal behaviour and disease ecology," *Proceedings of the Royal Society of London B: Biological Sciences*, **283**.
- [96] LOEHLE, C. (1995) "Social barriers to pathogen transmission in wild animal populations," *Ecology*, **76**(2), pp. 326–335.
- [97] CREMER, S., S. A. ARMITAGE, and P. SCHMID-HEMPEL (2007) "Social immunity," *Current Biology*, **17**(16), pp. R693–R702.
- [98] WILSON-RICH, N., M. SPIVAK, N. H. FEFFERMAN, and P. T. STARKS (2009) "Genetic, individual, and group facilitation of disease resistance in insect societies," *Annual Review of Entomology*, **54**, pp. 405–423.
- [99] CREMER, S., C. D. PULL, and M. A. FÜRST (2017) "Social immunity: emergence and evolution of colony-level disease protection," *Annual Review of Entomology*, (63), pp. 105–123.
- [100] SCHMID-HEMPEL, P. (2005) "Evolutionary ecology of insect immune defenses," *Annual Review of Entomology*, **50**, pp. 529–551.
- [101] SADD, B. M. and P. SCHMID-HEMPEL (2006) "Insect immunity shows specificity in protection upon secondary pathogen exposure," *Current Biology*, **16**(12), pp. 1206–1210.
- [102] MÜLLER, U., P. VOGEL, G. ALBER, and G. A. SCHAUB (2008) *The innate immune system of mammals and insects*, vol. 15, Karger Publishers, pp. 21–44.
- [103] COOPER, D. and I. ELEFThERIANOS (2017) "Memory and specificity in the insect immune system: current perspectives and future challenges," *Frontiers in Immunology*, **8**, p. 539.
- [104] ROSENGAUS, R. B., J. F. TRANIELLO, T. CHEN, J. J. BROWN, and R. D. KARP (1999) "Immunity in a social insect," *Naturwissenschaften*, **86**(12), pp. 588–591.
- [105] TIDBURY, H. J., A. B. PEDERSEN, and M. BOOTS (2011) "Within and transgenerational immune priming in an insect to a DNA virus," *Proceedings of the Royal Society of London B: Biological Sciences*, **278**(1707), pp. 871–876.

- [106] ROSENGAUS, R. B., T. MALAK, and C. MACKINTOSH (2013) “Immune-priming in ant larvae: social immunity does not undermine individual immunity,” *Biology Letters*, **9**(6), p. 20130563.
- [107] REBER, A. and M. CHAPUISAT (2012) “Diversity, prevalence and virulence of fungal entomopathogens in colonies of the ant *Formica selysi*,” *Insectes sociaux*, **59**(2), pp. 231–239.
- [108] SADD, B. M., Y. KLEINLOGEL, R. SCHMID-HEMPEL, and P. SCHMID-HEMPEL (2005) “Trans-generational immune priming in a social insect,” *Biology Letters*, **1**(4), pp. 386–388.
- [109] MORET, Y. (2006) “‘Trans-generational immune priming’: specific enhancement of the antimicrobial immune response in the mealworm beetle, *Tenebrio molitor*,” *Proceedings of the Royal Society of London B: Biological Sciences*, **273**(1592), pp. 1399–1405.
- [110] ROTH, O., G. JOOP, H. EGGERT, J. HILBERT, J. DANIEL, P. SCHMID-HEMPEL, and J. KURTZ (2010) “Paternally derived immune priming for offspring in the red flour beetle, *Tribolium castaneum*,” *Journal of Animal Ecology*, **79**(2), pp. 403–413.
- [111] TRAUER, U. and M. HILKER (2013) “Parental legacy in insects: variation of transgenerational immune priming during offspring development,” *PLoS One*, **8**(5), p. e63392.
- [112] LÓPEZ, J. H., W. SCHUEHLY, K. CRAILSHEIM, and U. RIESSBERGER-GALLÉ (2014) “Trans-generational immune priming in honeybees,” *Proceedings of the Royal Society of London B: Biological Sciences*, **281**, p. 20140454.
- [113] DUBUFFET, A., C. ZANCHI, G. BOUTET, J. MOREAU, M. TEIXEIRA, and Y. MORET (2015) “Trans-generational immune priming protects the eggs only against Gram-positive bacteria in the mealworm beetle,” *PLoS Pathogens*, **11**(10), p. e1005178.
- [114] TATE, A. T., P. ANDOLFATTO, J. P. DEMUTH, and A. L. GRAHAM (2017) “The within-host dynamics of infection in trans-generationally primed flour beetles,” *Molecular Ecology*, **26**(14), pp. 3794–3807.
- [115] MILUTINOVIĆ, B. and J. KURTZ (2016) “Immune memory in invertebrates,” *Seminars in Immunology*, **28**, pp. 328–342.
- [116] KURTZ, J. and S. A. ARMITAGE (2017) “Dissecting the dynamics of trans-generational immune priming,” *Molecular Ecology*, **26**(15), pp. 3857–3859.

- [117] SCHLUNS, H. and R. H. CROZIER (2009) “Molecular and chemical immune defenses in ants (Hymenoptera: Formicidae),” *Myrmecological News*, **12**, pp. 237–249.
- [118] HÖLLDOBLER, B. and H. ENGEL-SIEGEL (1984) “On the metapleural gland of ants,” *Psyche: a Journal of Entomology*, **91**(3-4), pp. 201–224.
- [119] YEK, S. H. and U. G. MUELLER (2011) “The metapleural gland of ants,” *Biological Reviews*, **86**(4), pp. 774–791.
- [120] DO NASCIMENTO, R. R., E. SCHOETERS, E. D. MORGAN, J. BILLEN, and D. J. STRADLING (1996) “Chemistry of metapleural gland secretions of three attine ants, *Atta sexdens rubropilosa*, *Atta cephalotes*, and *Acromyrmex octospinosus* (Hymenoptera: Formicidae),” *Journal of Chemical Ecology*, **22**(5), pp. 987–1000.
- [121] FERNÁNDEZ-MARÍN, H., J. K. ZIMMERMAN, S. A. REHNER, and W. T. WCISLO (2006) “Active use of the metapleural glands by ants in controlling fungal infection,” *Proceedings of the Royal Society of London B: Biological Sciences*, **273**(1594), pp. 1689–1695.
- [122] POULSEN, M., A. N. BOT, M. G. NIELSEN, and J. J. BOOMSMA (2002) “Experimental evidence for the costs and hygienic significance of the antibiotic metapleural gland secretion in leaf-cutting ants,” *Behavioral Ecology and Sociobiology*, **52**(2), pp. 151–157.
- [123] STOREY, G. K., R. K. VANDER MEER, D. G. BOUCIAS, and C. W. MCCOY (1991) “Effect of fire ant (*Solenopsis invicta*) venom alkaloids on the in vitro germination and development of selected entomogenous fungi,” *Journal of Invertebrate Pathology*, **58**(1), pp. 88–95.
- [124] ORIVEL, J., V. REDEKER, J.-P. LE CAER, F. KRIER, A.-M. REVOL-JUNELLES, A. LONGEON, A. CHAFFOTTE, A. DEJEAN, and J. ROSSIER (2001) “Ponericins, new antibacterial and insecticidal peptides from the venom of the ant *Pachycondyla goeldii*,” *Journal of Biological Chemistry*, **276**(21), pp. 17823–17829.
- [125] GRAYSTOCK, P. and W. O. HUGHES (2011) “Disease resistance in a weaver ant, *Polyrhachis dives*, and the role of antibiotic-producing glands,” *Behavioral Ecology and Sociobiology*, **65**(12), pp. 2319–2327.
- [126] BOS, N., L. SUNDSTRÖM, S. FUCHS, and D. FREITAK (2015) “Ants medicate to fight disease,” *Evolution*, **69**(11), pp. 2979–2984.
- [127] BOOMSMA, J., P. SCHMID-HEMPEL, and W. HUGHES (2005) *Life histories and parasite pressure across the major groups of social insects*, vol. 211, chap. 6, Royal Entomological Society, pp. 139–139.

- [128] COTTER, S. and R. KILNER (2010) “Personal immunity versus social immunity,” *Behavioral Ecology*, **21**(4), pp. 663–668.
- [129] STROEYMEYT, N., B. CASILLAS-PÉREZ, and S. CREMER (2014) “Organisational immunity in social insects,” *Current Opinion in Insect Science*, **5**, pp. 1–15.
- [130] DE SOUZA, D. J., J. VAN VLAENDEREN, Y. MORET, and A. LENOIR (2008) “Immune response affects ant trophallactic behaviour,” *Journal of Insect Physiology*, **54**(5), pp. 828–832.
- [131] QIU, H.-L., L.-H. LU, M. ZALUCKI, and Y.-R. HE (2016) “*Metarhizium anisopliae* infection alters feeding and trophallactic behavior in the ant *Solenopsis invicta*,” *Journal of Invertebrate Pathology*, **138**, pp. 24–29.
- [132] HAMILTON, C., B. T. LEJEUNE, and R. B. ROSENGAUS (2011) “Trophallaxis and prophylaxis: social immunity in the carpenter ant *Camponotus pennsylvanicus*,” *Biology Letters*, **7**(1), pp. 89–92.
- [133] KONRAD, M., M. L. VYLETA, F. J. THEIS, M. STOCK, S. TRAGUST, M. KLATT, V. DRESCHER, C. MARR, L. V. UGELVIG, and S. CREMER (2012) “Social transfer of pathogenic fungus promotes active immunisation in ant colonies,” *PLoS Biology*, **10**(4), p. e1001300.
- [134] KONRAD, M., C. D. PULL, K. SEIF, S. METZLER, A. V. GRASSE, and S. CREMER (2017) “Ants express risk-adjusted sanitary care,” *bioRxiv*, p. 170365.
- [135] MIRABITO, D. and R. ROSENGAUS (2016) “A double-edged sword? The cost of proctodeal trophallaxis in termites,” *Insectes Sociaux*, **63**(1), pp. 135–141.
- [136] ROSENGAUS, R. B., A. B. MAXMEN, L. E. COATES, and J. F. TRANIELLO (1998) “Disease resistance: a benefit of sociality in the dampwood termite *Zootermopsis angusticollis* (Isoptera: Termopsidae),” *Behavioral Ecology and Sociobiology*, **44**(2), pp. 125–134.
- [137] ROSENGAUS, R., J. TRANIELLO, M. LEFEBVRE, and D. CARLOCK (2000) “The social transmission of disease between adult male and female reproductives of the dampwood termite *Zootermopsis angusticollis*,” *Ethology, Ecology & Evolution*, **12**(4), pp. 419–433.
- [138] WALKER, T. N. and W. O. HUGHES (2009) “Adaptive social immunity in leaf-cutting ants,” *Biology Letters*.
- [139] REBER, A., J. PURCELL, S. BUECHEL, P. BURI, and M. CHAPUISAT (2011) “The expression and impact of antifungal grooming in ants,” *Journal of Evolutionary Biology*, **24**(5), pp. 954–964.

- [140] THEIS, F. J., L. V. UGELVIG, C. MARR, and S. CREMER (2015) “Opposing effects of allogrooming on disease transmission in ant societies,” *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **370**(1669), p. 20140108.
- [141] UGELVIG, L. V. and S. CREMER (2007) “Social prophylaxis: group interaction promotes collective immunity in ant colonies,” *Current Biology*, **17**(22), pp. 1967–1971.
- [142] RUEPPELL, O., M. HAYWORTH, and N. ROSS (2010) “Altruistic self-removal of health-compromised honey bee workers from their hive,” *Journal of Evolutionary Biology*, **23**(7), pp. 1538–1546.
- [143] BOS, N., T. LEFEVRE, A. JENSEN, and P. D’ETTORRE (2012) “Sick ants become unsociable,” *Journal of Evolutionary Biology*, **25**(2), pp. 342–351.
- [144] BARACCHI, D., A. FADDA, and S. TURILLAZZI (2012) “Evidence for antiseptic behaviour towards sick adult bees in honey bee colonies,” *Journal of Insect Physiology*, **58**(12), pp. 1589–1596.
- [145] BIGANSKI, S., C. KURZE, M. Y. MÜLLER, and R. F. MORITZ (2017) “Social response of healthy honeybees towards *Nosema ceranae*-infected workers: care or kill?” *Apidologie*, pp. 1–10.
- [146] PULL, C. D., L. V. UGELVIG, F. WIESENHOFER, A. V. GRASSE, S. TRAGUST, T. SCHMITT, M. J. BROWN, and S. CREMER (2018) “Destructive disinfection of infected brood prevents systemic disease spread in ant colonies,” *eLife*, **7**.
- [147] SUN, Q. and X. ZHOU (2013) “Corpse management in social insects,” *International Journal of Biological Sciences*, **9**(3), p. 313.
- [148] WILSON, E. O., N. I. DURLACH, and L. M. ROTH (1958) “Chemical releasers of necrophoric behavior in ants,” *Psyche: a Journal of Entomology*, **65**(4), pp. 108–114.
- [149] RENUCCI, M., A. TIRARD, and E. PROVOST (2011) “Complex undertaking behavior in *Temnothorax lichtensteini* ant colonies: from corpse-burying behavior to necrophoric behavior,” *Insectes Sociaux*, **58**(1), pp. 9–16.
- [150] DIEZ, L., J.-L. DENEUBOURG, and C. DETRAIN (2012) “Social prophylaxis through distant corpse removal in ants,” *Naturwissenschaften*, **99**(10), pp. 833–842.
- [151] DIEZ, L., H. LE BORGNE, P. LEJEUNE, and C. DETRAIN (2013) “Who brings out the dead? Necrophoresis in the red ant, *Myrmica rubra*,” *Animal Behaviour*, **86**(6), pp. 1259–1264.

- [152] MERSCH, D. P., A. CRESPI, and L. KELLER (2013) “Tracking individuals shows spatial fidelity is a key regulator of ant social organization,” *Science*, **340**(6136), pp. 1090–1093.
- [153] BARACCHI, D. and A. CINI (2014) “A socio-spatial combined approach confirms a highly compartmentalised structure in honeybees,” *Ethology*, **120**(12), pp. 1167–1176.
- [154] NAUG, D. and S. CAMAZINE (2002) “The role of colony organization on pathogen transmission in social insects,” *Journal of Theoretical Biology*, **215**(4), pp. 427–439.
- [155] PIE, M. R., R. B. ROSENGAUS, and J. F. TRANIELLO (2004) “Nest architecture, activity pattern, worker density and the dynamics of disease transmission in social insects,” *Journal of Theoretical Biology*, **226**(1), pp. 45–51.
- [156] FEFFERMAN, N. H., J. F. TRANIELLO, R. B. ROSENGAUS, and D. V. CALLERI II (2007) “Disease prevention and resistance in social insects: modeling the survival consequences of immunity, hygienic behavior, and colony organization,” *Behavioral Ecology and Sociobiology*, **61**(4), pp. 565–577.
- [157] HOCK, K. and N. H. FEFFERMAN (2012) “Social organization patterns can lower disease risk without associated disease avoidance or immunity,” *Ecological Complexity*, **12**, pp. 34–42.
- [158] WILSON, E. O. (1990) *Success and dominance in ecosystems: the case of the social insects*, Ecology Institute.
- [159] THOMAS, F., S. ADAMO, and J. MOORE (2005) “Parasitic manipulation: where are we and where should we go?” *Behavioural Processes*, **68**(3), pp. 185–199.
- [160] HUDSON, P. J., A. P. DOBSON, and K. D. LAFFERTY (2006) “Is a healthy ecosystem one that is rich in parasites?” *Trends in Ecology & Evolution*, **21**(7), pp. 381–385.
- [161] HATCHER, M. J., J. T. DICK, and A. M. DUNN (2012) “Diverse effects of parasites in ecosystems: linking interdependent processes,” *Frontiers in Ecology and the Environment*, **10**(4), pp. 186–194.
- [162] POULIN, R. (1995) “Phylogeny, ecology, and the richness of parasite communities in vertebrates,” *Ecological Monographs*, **65**(3), pp. 283–302.
- [163] ——— (2011) *Evolutionary Ecology of Parasites*, Princeton University Press.
- [164] SCHMID-HEMPEL, P. (2011) *Evolutionary Parasitology: the Integrated Study of Infections, Immunology, Ecology, and Genetics*.

- [165] EGGLETON, P. and K. J. GASTON (1990) “‘Parasitoid’ species and assemblages: convenient definitions or misleading compromises?” *Oikos*, pp. 417–421.
- [166] LAFFERTY, K. D. and A. M. KURIS (2002) “Trophic strategies, animal diversity and body size,” *Trends in Ecology & Evolution*, **17**(11), pp. 507–513.
- [167] ANDERSON, R. M. and R. M. MAY (1979) “Population biology of infectious diseases: Part I,” *Nature*, **280**(5721), p. 361.
- [168] GODFRAY, H. C. J. (1994) *Parasitoids: behavioral and evolutionary ecology*, Princeton University Press.
- [169] LAFFERTY, K. D., G. DELEO, C. J. BRIGGS, A. P. DOBSON, T. GROSS, and A. M. KURIS (2015) “A general consumer-resource population model,” *Science*, **349**(6250), pp. 854–857.
- [170] SHERMAN, P. W., T. D. SEELEY, and H. K. REEVE (1988) “Parasites, pathogens, and polyandry in social Hymenoptera,” *The American Naturalist*, **131**(4), pp. 602–610.
- [171] ANDERSEN, S. B., S. GERRITSMA, K. M. YUSAH, D. MAYNTZ, N. L. HYWEL-JONES, J. BILLEN, J. J. BOOMSMA, and D. P. HUGHES (2009) “The life of a dead ant: the expression of an adaptive extended phenotype,” *The American Naturalist*, **174**(3), pp. 424–433.
- [172] BEANI, L., D. MARCHINI, F. CAPPÀ, I. PETROCELLI, M. GOTTARDO, F. MANFREDINI, F. GIUSTI, and R. DALLAI (2017) “Subtle effect of *Xenos vesparum* (Xenidae, Strepsiptera) on the reproductive apparatus of its male host: Parasite or parasitoid?” *Journal of Insect Physiology*, **101**, pp. 22–30.
- [173] KRONAUER, D. J. and N. E. PIERCE (2011) “Myrmecophiles,” *Current Biology*, **21**(6), pp. R208–R209.
- [174] THOMAS, J. A., K. SCHÖNRÖGGE, and G. W. ELMES (2005) “Specializations and host associations of social parasites of ants,” *Insect Evolutionary Ecology*, pp. 479–518.
- [175] FRANKS, N. R., B. IRELAND, and A. F. BOURKE (1990) “Conflicts, social economics and life history strategies in ants,” *Behavioral Ecology and Sociobiology*, **27**(3), pp. 175–181.
- [176] WILSON, E. O. (1968) “The ergonomics of caste in the social insects,” *The American Naturalist*, **102**(923), pp. 41–66.
- [177] LAFFERTY, K. D. (1999) “The evolution of trophic transmission,” *Parasitology Today*, **15**(3), pp. 111–115.

- [178] POINAR, G. O. (1975) *Entomogenous Nematodes: A Manual and Host List of Insect-Nematode Associations*, Brill Archive.
- [179] DISNEY, R. (1994) *Scuttle Flies: The Phoridae*, Springer, Dordrecht.
- [180] KATHIRITHAMBY, J. (2009) "Host-parasitoid associations in Strepsiptera," *Annual Review of Entomology*, **54**.
- [181] LACHAUD, J.-P. and G. PÉREZ-LACHAUD (2012) "Diversity of species and behavior of hymenopteran parasitoids of ants: a review," *Psyche: a Journal of Entomology*, **2012**.
- [182] NOYES, J. (2017) *Universal Chalcidoidea Database*, Natural History Museum.
- [183] KATHIRITHAMBY, J. (2017) *Strepsiptera Database*.
- [184] BROWN, B. V. (2018) *Phorid Catalog*.
- [185] HANDOO, Z. and J. MOWERY (2017) *USDA Nematode Collection*.
- [186] ROSKOV, Y., T. KUNZE, L. PAGLINAWAN, T. ORRELL, D. NICOLSON, A. CULHAM, N. BAILLY, P. KIRK, T. BOURGOIN, G. BAILLARGEON, ET AL. (2016) "Species 2000 & ITIS Catalogue of Life, 2016 Annual Checklist," .
- [187] BAILEY, L. (1976) *Viruses attacking the honey bee*, vol. 20, Elsevier, pp. 271–304.
- [188] ALLEN, M. and B. BALL (1996) "The incidence and world distribution of honey bee viruses," *Bee World*, **77**(3), pp. 141–162.
- [189] ELLIS, J. D. and P. A. MUNN (2005) "The worldwide health status of honey bees," *Bee World*, **86**(4), pp. 88–101.
- [190] CHEN, Y. P. and R. SIEDE (2007) "Honey bee viruses," *Advances in Virus Research*, **70**, pp. 33–80.
- [191] STEIGER, U., H. LAMPARTER, C. SANDRI, and K. AKERT (1969) "Virus-ähnliche Partikel im Zytoplasma von Nerven- und Gliazellen der Waldameise," *Archiv für die gesamte Virusforschung*, **26**(3), pp. 271–282.
- [192] AVERY, S., D. JOUVENAZ, W. BANKS, and D. ANTHONY (1977) "Virus-like particles in a fire ant, *Solenopsis sp.*, (Hymenoptera: Formicidae) from Brazil," *Florida Entomologist*, pp. 17–20.
- [193] VALLES, S. M., C. A. STRONG, P. M. DANG, W. B. HUNTER, R. M. PEREIRA, D. H. OI, A. M. SHAPIRO, and D. F. WILLIAMS (2004) "A picorna-like virus from the red imported fire ant, *Solenopsis invicta*: initial discovery, genome sequence, and characterization," *Virology*, **328**(1), pp. 151–157.

- [194] VALLES, S. M., C. A. STRONG, D. H. OI, S. D. PORTER, R. M. PEREIRA, R. K. VANDER MEER, Y. HASHIMOTO, L. M. HOOPER-BÙI, H. SÁNCHEZ-ARROYO, and T. DAVIS (2007) “Phenology, distribution, and host specificity of *Solenopsis invicta* virus-1,” *Journal of Invertebrate Pathology*, **96**(1), pp. 18–27.
- [195] VALLES, S. M., L. VARONE, L. RAMÍREZ, and J. BRIANO (2009) “Multiplex detection of *Solenopsis invicta* viruses-1,-2, and-3,” *Journal of Virological Methods*, **162**(1-2), pp. 276–279.
- [196] VALLES, S. M. (2012) “Positive-strand RNA viruses infecting the red imported fire ant, *Solenopsis invicta*,” *Psyche: a Journal of Entomology*, **2012**.
- [197] CHEN, Y.-C., L. KAFLE, and C.-J. SHIH (2011) “Interspecific competition between *Solenopsis invicta* and two native ant species, *Pheidole fervens* and *Monomorium chinense*,” *Journal of Economic Entomology*, **104**(2), pp. 614–621.
- [198] VALLES, S. M. and Y. HASHIMOTO (2009) “Isolation and characterization of *Solenopsis invicta* virus 3, a new positive-strand RNA virus infecting the red imported fire ant, *Solenopsis invicta*,” *Virology*, **388**(2), pp. 354–361.
- [199] ALLEN, C., S. M. VALLES, and C. A. STRONG (2011) “Multiple virus infections occur in individual polygyne and monogyne *Solenopsis invicta* ants,” *Journal of Invertebrate Pathology*, **107**(2), pp. 107–111.
- [200] VALLES, S. M., S. D. PORTER, M.-Y. CHOI, and D. H. OI (2013) “Successful transmission of *Solenopsis invicta* virus 3 to *Solenopsis invicta* fire ant colonies in oil, sugar, and cricket bait formulations,” *Journal of Invertebrate Pathology*, **113**(3), pp. 198–204.
- [201] VALLES, S. M., S. D. PORTER, and A. E. FIRTH (2014) “*Solenopsis invicta* virus 3: pathogenesis and stage specificity in red imported fire ants,” *Virology*, **460**, pp. 66–71.
- [202] CELLE, O., P. BLANCHARD, V. OLIVIER, F. SCHURR, N. COUGOULE, J.-P. FAUCON, and M. RIBIÈRE (2008) “Detection of Chronic bee paralysis virus (CBPV) genome and its replicative RNA form in various hosts and possible ways of spread,” *Virus Research*, **133**(2), pp. 280–284.
- [203] GRUBER, M. A., M. COOLING, J. W. BATY, K. BUCKLEY, A. FRIEDLANDER, O. QUINN, J. F. RUSSELL, A. SÉBASTIEN, and P. J. LESTER (2017) “Single-stranded RNA viruses infecting the invasive Argentine ant, *Linepithema humile*,” *Scientific Reports*, **7**(1), p. 3304.
- [204] VALLES, S. M., D. SHOEMAKER, Y. WURM, C. A. STRONG, L. VARONE, J. J. BECNEL, and P. D. SHIRK (2013) “Discovery and molecular characterization of an

- ambisense densovirus from South American populations of *Solenopsis invicta*,” *Biological Control*, **67**(3), pp. 431–439.
- [205] JOUVENAZ, D., W. BANKS, and J. ATWOOD (1980) “Incidence of pathogens in fire ants, *Solenopsis spp.*, in Brazil,” *Florida Entomologist*, **63**(3), pp. 345–346.
- [206] BAIRD, R., S. WOOLFOLK, and C. WATSON (2007) “Survey of bacterial and fungal associates of black/hybrid imported fire ants from mounds in Mississippi,” *Southeastern Naturalist*, **6**(4), pp. 615–632.
- [207] ISHAK, H. D., R. PLOWES, R. SEN, K. KELLNER, E. MEYER, D. A. ESTRADA, S. E. DOWD, and U. G. MUELLER (2011) “Bacterial diversity in *Solenopsis invicta* and *Solenopsis geminata* ant colonies characterized by 16S amplicon 454 pyrosequencing,” *Microbial Ecology*, **61**(4), pp. 821–831.
- [208] POWELL, C. M., J. D. HANSON, and B. R. BEXTINE (2014) “Bacterial community survey of *Solenopsis invicta* Buren (red imported fire ant) colonies in the presence and absence of *Solenopsis invicta* virus (SINV),” *Current Microbiology*, **69**(4), pp. 580–585.
- [209] WOOLFOLK, S., C. E. STOKES, C. WATSON, R. BROWN, and R. BAIRD (2016) “Bacteria associated with red imported fire ants (*Solenopsis invicta*) from mounds in Mississippi,” *Southeastern Naturalist*, **15**(1), pp. 83–101.
- [210] LOFGREN, C., W. BANKS, and B. GLANCEY (1975) “Biology and control of imported fire ants,” *Annual Review of Entomology*, **20**(1), pp. 1–30.
- [211] WENSELEERS, T., L. SUNDSTRÖM, and J. BILLEN (2002) “Deleterious *Wolbachia* in the ant *Formica truncorum*,” *Proceedings of the Royal Society of London B: Biological Sciences*, **269**(1491), pp. 623–629.
- [212] VAN BORM, S., J. BILLEN, and J. J. BOOMSMA (2002) “The diversity of microorganisms associated with *Acromyrmex* leafcutter ants,” *BMC Evolutionary Biology*, **2**(1), p. 9.
- [213] KAUTZ, S., B. E. RUBIN, J. A. RUSSELL, and C. S. MOREAU (2013) “Surveying the microbiome of ants: comparing 454 pyrosequencing with traditional methods to uncover bacterial diversity,” *Applied and Environmental Microbiology*, **79**(2), pp. 525–534.
- [214] SAUER, C., E. STACHEBRANDT, J. GADAU, B. HÖLDOBLER, and R. GROSS (2000) “Systematic relationships and cospeciation of bacterial endosymbionts and their carpenter ant host species: proposal of the new taxon *Candidatus Blochmannia gen. nov.*” *International Journal of Systematic and Evolutionary Microbiology*, **50**(5), pp. 1877–1886.

- [215] FELDHAAR, H. (2011) “Bacterial symbionts as mediators of ecologically important traits of insect hosts,” *Ecological Entomology*, **36**(5), pp. 533–543.
- [216] FELDHAAR, H. and R. GROSS (2008) “Immune reactions of insects on bacterial pathogens and mutualists,” *Microbes and Infection*, **10**(9), pp. 1082–1088.
- [217] POINAR JR, G. O. (1990) *Biology and taxonomy of Steinernematidae and Heterorhabditidae*, Entomopathogenic Nematodes in Biological Control, CRC Press, Boca Raton, FL.
- [218] HAJEK, A. and R. ST. LEGER (1994) “Interactions between fungal pathogens and insect hosts,” *Annual Review of Entomology*, **39**(1), pp. 293–322.
- [219] CHAPELA, I. H., S. A. REHNER, T. R. SCHULTZ, and U. G. MUELLER (1994) “Evolutionary history of the symbiosis between fungus-growing ants and their fungi,” *Science*, **266**(5191), pp. 1691–1694.
- [220] AANEN, D. K., P. EGGLETON, C. ROULAND-LEFEVRE, T. GULDBERG-FRØSLEV, S. ROSENDAHL, and J. J. BOOMSMA (2002) “The evolution of fungus-growing termites and their mutualistic fungal symbionts,” *Proceedings of the National Academy of Sciences*, **99**(23), pp. 14887–14892.
- [221] SCHULTZ, T. R. and S. G. BRADY (2008) “Major evolutionary transitions in ant agriculture,” *Proceedings of the National Academy of Sciences*, **105**(14), pp. 5435–5440.
- [222] HUGHES, D. P., T. WAPPLER, and C. C. LABANDEIRA (2010) “Ancient death-grip leaf scars reveal ant-fungal parasitism,” *Biology Letters*.
- [223] MADELIN, M. (1966) *The fungus spore*.
- [224] EVANS, H. C. (2001) *Entomopathogenic fungi associated with ants (Formicidae): A review*, Science Publishers.
- [225] ESPADALER, X. and S. SANTAMARIA (2012) “Ecto- and endoparasitic fungi on ants from the Holarctic region,” *Psyche: a Journal of Entomology*, **2012**.
- [226] BUTT, T., C. COATES, I. DUBOVSKIY, and N. RATCLIFFE (2016) *Entomopathogenic fungi: new insights into host–pathogen interactions*, vol. 94, Elsevier, pp. 307–364.
- [227] ARAÚJO, J. P. and D. P. HUGHES (2016) *Diversity of entomopathogenic fungi: which groups conquered the insect body?*, vol. 94, Elsevier, pp. 1–39.

- [228] WOOLFOLK, S., C. E. STOKES, C. WATSON, G. BAKER, R. BROWN, and R. BAIRD (2016) "Fungi associated with *Solenopsis invicta* Buren (Red imported fire ant, Hymenoptera: Formicidae) from mounds in Mississippi," *Southeastern Naturalist*, **15**(2), pp. 220–234.
- [229] BEQUAERT, J. C. (1922) *Ants in their diverse relations to the plant world*, vol. 45, American Museum of Natural History, New York.
- [230] EVANS, H. (1974) "Natural control of arthropods, with special reference to ants (Formicidae), by fungi in the tropical high forest of Ghana," *Journal of Applied Ecology*, pp. 37–49.
- [231] LORETO, R. G., S. L. ELLIOT, M. L. FREITAS, T. M. PEREIRA, and D. P. HUGHES (2014) "Long-term disease dynamics for a specialized parasite of ant societies: a field study," *PloS One*, **9**(8), p. e103516.
- [232] LORETO, R. and D. HUGHES (2016) "Disease Dynamics in Ants: A Critical Review of the Ecological Relevance of Using Generalist Fungi to Study Infections in Insect Societies," *Advances in Genetics*, **94**, pp. 287–306.
- [233] KEVORKIAN, A. G. (1937) *Studies in the Entomophthoraceae: Observations on the Genus Conidiobolus. I*, Harvard University. Laboratories of Cryptogamic Botany.
- [234] YENDOL, W. G. and J. D. PASCHKE (1965) "Pathology of an *Entomophthora* infection in the eastern subterranean termite *Reticulitermes flavipes* (Kollar)," *Journal of Invertebrate Pathology*, **7**(4), pp. 414–422.
- [235] HUMBER, R., C. BROWN, and R. KORNEGAY (1989) "Equine zygomycosis caused by *Conidiobolus lamprauges*," *Journal of Clinical Microbiology*, **27**(3), pp. 573–576.
- [236] SANCHEZ-PENA, S. and H. THORVILSON (1992) "Two fungi infecting red imported fire ant founding queens from Texas," *The Southwestern Entomologist*.
- [237] MARIKOVSKY, P. (1962) "On some features of behavior of the ants *Formica rufa* L. infected with fungous disease," *Insectes Sociaux*, **9**(2), pp. 173–179.
- [238] MAŁAGOCKA, J., A. B. JENSEN, and J. EILENBERG (2017) "*Pandora formicae*, a specialist ant pathogenic fungus: new insights into biology and taxonomy," *Journal of Invertebrate Pathology*, **143**, pp. 108–114.
- [239] CSATA, E., Z. CZEKES, K. ERŐS, E. NÉMET, M. HUGHES, S. CSÓSZ, and B. MARKO (2013) "Comprehensive survey of Romanian myrmecoparasitic fungi: new species, biology and distribution," *North-Western Journal of Zoology*.
- [240] BOER, P. (2008) "Observations of summit disease in *Formica rufa* Linnaeus, 1761 (Hymenoptera: Formicidae)," *Myrmecological News*, (11), pp. 63–66.

- [241] HUGHES, D. P., S. B. ANDERSEN, N. L. HYWEL-JONES, W. HIMAMAN, J. BILLEN, and J. J. BOOMSMA (2011) "Behavioral mechanisms and morphological symptoms of zombie ants dying from fungal infection," *BMC Ecology*, **11**(1), p. 13.
- [242] RODRIGUES, A., D. R. SOLIS, E. G. FOX, F. C. PAGNOCCA, and O. C. BUENO (2010) "Preliminary list of microfungi found in *Paratrechina longicornis* (Hymenoptera: Formicidae)," *Florida Entomologist*, **93**(4), pp. 651–653.
- [243] DE HOOG, G. S. and G. DE HOOG (1974) *The genera Blastobotrys, Sporothrix, Calcarisporium and Calcarisporiella gen. nov.*, Centraalbureau voor Schimmelcultures.
- [244] BALAZY, S. and A. SOKOŁOWSKI (1977) "Morphology and biology of *Entomophthora myrmecophaga*," *Transactions of the British Mycological Society*, **68**(1), pp. 134–137.
- [245] BOOTH, C. ET AL. (1971) "The genus *Fusarium*." *The genus Fusarium*.
- [246] TEETOR-BARSCH, G. and W. ROBERTS (1983) "Fusarium species pathogens of insects. Review," *Mycopathologia*, **84**, pp. 3–16.
- [247] VEGA, F. E. and M. BLACKWELL (2005) *Insect-fungal associations: ecology and evolution*, Oxford University Press.
- [248] LEGER, R. J. S. (2008) "Studies on adaptations of *Metarhizium anisopliae* to life in the soil," *Journal of Invertebrate Pathology*, **98**(3), pp. 271–276.
- [249] PETCH, T. (1931) "Notes on entomogenous fungi," *Transactions of the British Mycological Society*, **16**(1), pp. 55–75.
- [250] SUNG, G.-H., N. L. HYWEL-JONES, J.-M. SUNG, J. J. LUANGSA-ARD, B. SHRESTHA, and J. W. SPATAFORA (2007) "Phylogenetic classification of *Cordyceps* and the clavicipitaceous fungi," *Studies in Mycology*, **57**, pp. 5–59.
- [251] INGLIS, G. D., M. S. GOETTEL, T. M. BUTT, and H. STRASSER (2001) "Use of hyphomycetous fungi for managing insect pests," *Fungi as biocontrol agents*, pp. 23–69.
- [252] MEYLING, N. V. and J. EILENBERG (2007) "Ecology of the entomopathogenic fungi *Beauveria bassiana* and *Metarhizium anisopliae* in temperate agroecosystems: potential for conservation biological control," *Biological control*, **43**(2), pp. 145–155.
- [253] REHNER, S. A. and E. BUCKLEY (2005) "A *Beauveria* phylogeny inferred from nuclear ITS and EF1-1 sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs," *Mycologia*, **97**(1), pp. 84–98.

- [254] ANDERSEN, S. B., M. FERRARI, H. C. EVANS, S. L. ELLIOT, J. J. BOOMSMA, and D. P. HUGHES (2012) “Disease dynamics in a specialized parasite of ant societies,” *PloS One*, **7**(5), p. e36352.
- [255] DE BEKKER, C., L. E. QUEVILLON, P. B. SMITH, K. R. FLEMING, D. GHOSH, A. D. PATTERSON, and D. P. HUGHES (2014) “Species-specific ant brain manipulation by a specialized fungal parasite,” *BMC Evolutionary Biology*, **14**(1), p. 166.
- [256] DE BEKKER, C., R. A. OHM, R. G. LORETO, A. SEBASTIAN, I. ALBERT, M. MERROW, A. BRACHMANN, and D. P. HUGHES (2015) “Gene expression during zombie ant biting behavior reflects the complexity underlying fungal parasitic behavioral manipulation,” *BMC Genomics*, **16**(1), p. 620.
- [257] FREDERICKSEN, M. A., Y. ZHANG, M. L. HAZEN, R. G. LORETO, C. A. MANGOLD, D. Z. CHEN, and D. P. HUGHES (2017) “Three-dimensional visualization and a deep-learning model reveal complex fungal parasite networks in behaviorally manipulated ants,” *Proceedings of the National Academy of Sciences*, p. 201711673.
- [258] ARAÚJO, J. P., H. C. EVANS, R. KEPLER, and D. P. HUGHES (2018) “Zombie-ant fungi across continents: 15 new species and new combinations within *Ophiocordyceps*. I. Myrmecophilous hirsutelloid species,” *Studies in Mycology*.
- [259] TAYLOR, J. W. (2011) “One fungus= one name: DNA and fungal nomenclature twenty years after PCR,” *IMA fungus*, **2**(2), pp. 113–120.
- [260] EVANS, H. C., S. L. ELLIOT, and D. P. HUGHES (2011) “Hidden diversity behind the zombie-ant fungus *Ophiocordyceps unilateralis*: four new species described from carpenter ants in Minas Gerais, Brazil,” *PloS One*, **6**(3), p. e17024.
- [261] ARAÚJO, J. P. M., H. C. EVANS, D. M. GEISER, W. P. MACKAY, and D. P. HUGHES (2015) “Unravelling the diversity behind the *Ophiocordyceps unilateralis* (Ophiocordycipitaceae) complex: Three new species of zombie-ant fungi from the Brazilian Amazon,” *Phytotaxa*, **220**(3), pp. 224–238.
- [262] CHÉRIX, D. (1982) “Note sur la presence d’*Aegeritella superficialis* Bal. & Wis.(Hyphomycetales, Blastoporaes) sur des especes du genre *Formica* (Hymenoptera, Formicidae) en Suisse,” *Bulletin de la Societe Entomologique Suisse*.
- [263] WISNIEWSKI, J. and A. BUSCHINGER (1982) “*Aegeritella superficialis* Bal. et Wis. an epizootic fungus on forest-ants in the Federal Republic of Germany. [German],” *Waldhygiene*.
- [264] JOUVENAZ, D. and J. KIMBROUGH (1991) “*Myrmecomyces annellisae* gen. nov., sp. nov. (Deuteromycotina: Hyphomycetes), an endoparasitic fungus of fire ants,

- Solenopsis* spp. (Hymenoptera: Formicidae),” *Mycological Research*, **95**(12), pp. 1395–1401.
- [265] SANCHEZ-PEÑA, S. R., A. BUSCHINGER, and R. A. HUMBER (1993) “*Myrmicinosporidium durum*, an enigmatic fungal parasite of ants,” *Journal of Invertebrate Pathology*, **61**(1), pp. 90–96.
- [266] PEREIRA, R. M. (2004) “Occurrence of *Myrmicinosporidium durum* in red imported fire ant, *Solenopsis invicta*, and other new host ants in eastern United States,” *Journal of Invertebrate Pathology*, **86**(1-2), pp. 38–44.
- [267] CSÓSZ, S., A. LAPEVA-GJONOVA, B. MARKÓ, and H. HAGEDORN (2012) “New data on the geographical distribution and host utilization of the entomopathogenic fungus *Myrmicinosporidium durum*,” *Journal of insect science*, **12**(1).
- [268] GONÇALVES, C., I. PATANITA, and X. ESPADALER (2012) “Substantial, and significant, expansion of ant hosts range for *Myrmicinosporidium* Hölldobler, 1933 (Fungi),” *Insectes Sociaux*, **59**(3), pp. 395–399.
- [269] HÖLLDOBLER, K. (1927) “Über merkwürdige Parasiten von *Solenopsis fugax*,” *Zoologischer Anzeiger*, **70**, pp. 333–334.
- [270] ——— (1933) “Weitere Mitteilungen über Haplosporidien in Ameisen,” *Parasitology Research*, **6**(1), pp. 91–100.
- [271] KEELING, P. J. and N. M. FAST (2002) “Microsporidia: biology and evolution of highly reduced intracellular parasites,” *Annual Reviews in Microbiology*, **56**(1), pp. 93–116.
- [272] HIRT, R. P., J. M. LOGSDON, B. HEALY, M. W. DOREY, W. F. DOOLITTLE, and T. M. EMBLEY (1999) “Microsporidia are related to Fungi: evidence from the largest subunit of RNA polymerase II and other proteins,” *Proceedings of the National Academy of Sciences*, **96**(2), pp. 580–585.
- [273] JOUVENAZ, D. and E. HAZARD (1978) “New family, genus, and species of microsporida (Protozoa: Microsporida) from the tropical fire ant, *Solenopsis geminata* (Fabricius) (Insecta: Formicidae),” *Journal of Eukaryotic Microbiology*, **25**(1), pp. 24–29.
- [274] JOUVENAZ, D., C. LOFGREN, and G. ALLEN (1981) “Transmission and infectivity of spores of *Burenella dimorpha* (Microsporida: Burenellidae),” *Journal of Invertebrate Pathology*, **37**(3), pp. 265–268.
- [275] JOUVENAZ, D. P. and E. ELLIS (1986) “*Vairimorpha invictae* n. sp. (Microspora: Microsporida), a parasite of the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae),” *Journal of Eukaryotic Microbiology*, **33**(4), pp. 457–461.

- [276] BRIANO, J. A., D. WILLIAMS, D. OI, and L. DAVIS (2002) "Field host range of the fire ant pathogens *Thelohania solenopsae* (Microsporida: Thelohaniidae) and *Vairimorpha invictae* (Microsporida: Burenellidae) in South America," *Biological Control*, **24**(1), pp. 98–102.
- [277] ALLEN, G. E. and W. F. BUREN (1974) "Microsporidan and fungal diseases of *Solenopsis invicta* Buren in Brazil," *Journal of the New York Entomological Society*, pp. 125–130.
- [278] ALLEN, G. E. and A. SILVEIRA-GUIDO (1974) "Occurrence of microsporida in *Solenopsis richteri* and *Solenopsis sp.* in Uruguay and Argentina," *Florida Entomologist*, pp. 327–329.
- [279] BRIANO, J., R. PATTERSON, and H. CORDO (1995) "Long-term studies of the black imported fire ant (Hymenoptera: Formicidae) infected with a microsporidium," *Environmental Entomology*, **24**(5), pp. 1328–1332.
- [280] WILLIAMS, D. F., D. H. OI, and G. J. KNUE (1999) "Infection of red imported fire ant (Hymenoptera: Formicidae) colonies with the entomopathogen *Thelohania solenopsae* (Microsporidia: Thelohaniidae)," *Journal of Economic Entomology*, **92**(4), pp. 830–836.
- [281] SOKOLOVA, Y. and J. FUXA (2008) "Biology and life-cycle of the microsporidium *Kneallhazia solenopsae* Knell Allan Hazard 1977 gen. n., comb. n., from the fire ant *Solenopsis invicta*," *Parasitology*, **135**(8), pp. 903–929.
- [282] PEREIRA, R. M., D. F. WILLIAMS, J. J. BECNEL, and D. H. OI (2002) "Yellow-head disease caused by a newly discovered *Mattesia sp.* in populations of the red imported fire ant, *Solenopsis invicta*," *Journal of Invertebrate Pathology*, **81**(1), pp. 45–48.
- [283] JOUVENAZ, D. and D. ANTHONY (1979) "*Mattesia geminata sp. n.* (Neogregarinida: Ophrocystidae) a parasite of the tropical fire ant, *Solenopsis geminata* (Fabricius)," *Journal of Eukaryotic Microbiology*, **26**(3), pp. 354–356.
- [284] KLEESPIES, R., A. HUGER, A. BUSCHINGER, S. NÄHRING, and R. SCHUMANN (1997) "Studies on the life history of a neogregarine parasite found in *Leptothorax* ants from North America," *Biocontrol Science and Technology*, **7**(1), pp. 117–130.
- [285] ESCH, G. W., M. A. BARGER, and K. J. FELLIS (2002) "The transmission of digenetic trematodes: style, elegance, complexity," *Integrative and Comparative Biology*, **42**(2), pp. 304–312.
- [286] POULIN, R. (1998) *Evolutionary Ecology of Parasites-from Individuals to Communities*, Chapman Hall, London.

- [287] BUSH, A. O. (2001) *Parasitism: the diversity and ecology of animal parasites*, Cambridge University Press, Cambridge.
- [288] CARNEY, W. P. (1967) "Notes on the life cycle of *Brachylecithum mosquensis* (Skrjabin and Isaitschikoff, 1927) from the bile ducts of the robin, *Turdus migratorius*, in Montana," *Canadian Journal of Zoology*, **45**(1), pp. 131–134.
- [289] ——— (1969) "Behavioral and morphological changes in carpenter ants harboring dicrocoeliid metacercariae," *The American Midland Naturalist*, **82**(2), pp. 605–611.
- [290] MANGA-GONZÁLEZ, M., C. GONZÁLEZ-LANZA, E. CABANAS, and R. CAMPO (2001) "Contributions to and review of dicrocoeliosis, with special reference to the intermediate hosts of *Dicrocoelium dendriticum*," *Parasitology*, **123**(7), pp. 91–114.
- [291] KRULL, W. H. and C. R. MAPES (1952) "Studies on the biology of *Dicrocoelium dendriticum* (Rudolphi, 1819) looss, 1899 (Trematoda: Dicrocoeliidae), including its relation to the intermediate host, *Cionella lubrica* (Müller). VII. The second intermediate host of *Dicrocoelium dendriticum*," *Cornell Veterinarian*, **42**(4), pp. 603–604.
- [292] SVADZHYAN, P. and L. FROKOLVA (1966) "Ants as first and second intermediate hosts of some trematodes and cestodes," *Zoologicheskii Zhurnal*, **45**(2), pp. 213–219.
- [293] PADGETT, K. and W. BOYCE (2007) "Ants as first intermediate hosts of *Mesocostoides* on San Miguel Island, USA," *Journal of Helminthology*, **79**(1), pp. 67–73.
- [294] BLAXTER, M. L. (2003) "Nematoda: genes, genomes and the evolution of parasitism," *Advances in Parasitology*, **54**, pp. 101–195.
- [295] BLAXTER, M. and G. KOUTSOVOULOS (2015) "The evolution of parasitism in Nematoda," *Parasitology*, **142**(S1), pp. S26–S39.
- [296] POINAR JR, G. (2002) "First fossil record of nematode parasitism of ants; a 40 million year tale," *Parasitology*, **125**(5), pp. 457–459.
- [297] POINAR, G., J.-P. LACHAUD, A. CASTILLO, and F. INFANTE (2006) "Recent and fossil nematode parasites (Nematoda: Mermithidae) of Neotropical ants," *Journal of Invertebrate Pathology*, **91**(1), pp. 19–26.
- [298] POINAR, G. (2012) "Nematode parasites and associates of ants: past and present," *Psyche: a Journal of Entomology*, **2012**.

- [299] ——— (2003) “*Formicitylenchus oregonensis* ng, n. sp. (Allantonematidae: Nematoda), the first tylenchid parasite of ants, with a review of nematodes described from ants,” *Systematic Parasitology*, **56**(1), pp. 69–76.
- [300] POINAR, G. O. (2011) *The evolutionary history of nematodes: as revealed in stone, amber and mummies*, vol. 9, Brill, Leiden-Boston.
- [301] MARKIN, G. P. and C. W. MCCOY (1968) “The occurrence of a nematode, *Diploscapter lycostoma*, in the pharyngeal glands of the argentine ant, *Iridomyrmex humilis*,” *Annals of the Entomological Society of America*, **61**(2), pp. 505–509.
- [302] SUDHAUS, W. (2016) “The guild of saprobiontic nematodes associated with ants (Formicoidea),” *Ecologica Montenegrina*, **7**, pp. 600–613.
- [303] QUATTLEBAUM, E. C. (1980) “Evaluation of fungal and nematode pathogens to control the red imported fire ant, *Solenopsis invicta* Buren,” .
- [304] POINAR, G., A. CHABAUD, and O. BAIN (1989) “*Rabbiium paradoxus* sp. n. (Seuratidae: Skjabinelaziinae) maturing in *Camponotus castaneus* (Hymenoptera: Formicidae),” *Proceedings of the Helminthological Society of Washington*, **56**(2), pp. 120–124.
- [305] NICKLE, W. and G. AYRE (1966) “*Caenorhabditis dolichura* (A. Schneider, 1866) Dougherty (Rhabditidae, Nematoda) in the head glands of the ants *Camponotus herculeanus* (L.) and *Acanthomyops claviger* (Roger) in Ontario,” *Proceedings of the Entomological Society of Ontario*, **96**, pp. 96–98.
- [306] YANOVIK, S. P., M. KASPARI, R. DUDLEY, and G. POINAR JR (2008) “Parasite-induced fruit mimicry in a tropical canopy ant,” *The American Naturalist*, **171**(4), pp. 536–544.
- [307] MOORE, J. (2002) *Parasites and the behavior of animals*, Oxford University Press, New York.
- [308] WHITFIELD, J. (1998) “Phylogeny and evolution of host-parasitoid interactions in Hymenoptera,” *Annual Review of Entomology*, **43**(1), pp. 129–151.
- [309] WHITFIELD, J. B. (2003) “Phylogenetic insights into the evolution of parasitism in Hymenoptera,” *Advances in Parasitology*, **54**, pp. 69–101.
- [310] MURRAY, E. A., A. E. CARMICHAEL, and J. M. HERATY (2013) “Ancient host shifts followed by host conservatism in a group of ant parasitoids,” *Proceedings of the Royal Society of London B: Biological Sciences*, **280**(1759), p. 20130495.

- [311] FARRIS, S. M. and S. SCHULMEISTER (2011) "Parasitoidism, not sociality, is associated with the evolution of elaborate mushroom bodies in the brains of hymenopteran insects," *Proceedings of the Royal Society of London B: Biological Sciences*, **278**(1707), pp. 940–951.
- [312] EGGLETON, P. and R. BELSHAW (1992) "Insect parasitoids: an evolutionary overview," *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **337**(1279), pp. 1–20.
- [313] BROTHERS, D., G. TSCHUCH, and F. BURGER (2000) "Associations of mutillid wasps (Hymenoptera, Mutillidae) with eusocial insects," *Insectes Sociaux*, **47**(3), pp. 201–211.
- [314] BROTHERS, D. (2015) "Revision of the Rhopalomutillinae (Hymenoptera, Mutillidae): 1, generic review with descriptions of three new genera," *Journal of Hymenoptera Research*, **46**, p. 1.
- [315] BROTHERS, D. J. (1989) *Alternative life-history styles of mutillid wasps (Insecta, Hymenoptera)*, Springer, pp. 279–291.
- [316] ——— (1994) "A new genus and four new species of Mutillidae associated with *Brachyponera lutea* Mayr (Formicidae) in Western Australia (Hymenoptera)," *Austral Entomology*, **33**(2), pp. 143–152.
- [317] EVANS, H. E. (1964) "A synopsis of the American Bethylidae (Hymenoptera, Aculeata)," *Bulletin of the Museum of Comparative Zoology*, **132**, pp. 1–222.
- [318] MANN, W. M. (1915) "Some myrmecophilous insects from Hayti," *Psyche: a Journal of Entomology*, **22**(5), pp. 161–166.
- [319] BRUCH, C. (1917) "Nuevas capturas de insectos mirmecófilos," *Physis*, **3**(15), pp. 458–465.
- [320] DARLING, D. C. (2009) "A new species of *Smicromorpha* (Hymenoptera, Chalcididae) from Vietnam, with notes on the host association of the genus," *ZooKeys*, **20**, pp. 155–163.
- [321] GIRAULT, A. (1913) "New genera and species of chalcidoid Hymenoptera from North Queensland," *Archiv für Naturgeschichte*, **79**, pp. 46–51.
- [322] PÉREZ-LACHAUD, G., J. NOYES, and J.-P. LACHAUD (2012) "First record of an encyrtid wasp (Hymenoptera: Chalcidoidea) as a true primary parasitoid of ants (Hymenoptera: Formicidae)," *Florida Entomologist*, **95**(4), pp. 1066–1076.
- [323] CLAUSEN, C. P. (1940) "The oviposition habits of the Eucharidae (Hymenoptera)," *Journal of the Washington Academy of Sciences*, **30**(12), pp. 504–516.

- [324] HERATY, J. M. (2002) *Revision of the genera of Eucharitidae (Hymenoptera: Chalcidoidea) of the world*, American Entomological Institute.
- [325] HERATY, J., D. HAWKS, J. S. KOSTECKI, and A. CARMICHAEL (2004) "Phylogeny and behaviour of the Gollumiellinae, a new subfamily of the ant-parasitic Eucharitidae (Hymenoptera: Chalcidoidea)," *Systematic Entomology*, **29**(4), pp. 544–559.
- [326] HERATY, J. M., J. M. HERATY, and J. TORRÉNS (2009) "A new species of *Pseudochalcura* (Hymenoptera, Eucharitidae), with a review of antennal morphology from a phylogenetic perspective," *ZooKeys*, **20**, p. 215.
- [327] HERATY, J. (2014) "Catalog of World Eucharitidae, 2014," *University of California, Riverside*.
- [328] TORRÉNS, J. (2013) "A review of the biology of Eucharitidae (Hymenoptera: Chalcidoidea) from Argentina," *Psyche*, **2013**.
- [329] BOUČEK, Z. (1956) "A contribution to the knowledge of the Chalcididae, Leucospididae and Eucharitidae (Hymenoptera: Chalcidoidea) of the Near East," *Bulletin of the Research Council of Israel B*, **5**, pp. 227–259.
- [330] HERATY, J. M. and D. C. DARLING (1984) "Comparative morphology of the planidial larvae of Eucharitidae and Perilampidae (Hymenoptera: Chalcidoidea)," *Systematic Entomology*, **9**(3), pp. 309–328.
- [331] HERATY, J. and E. MURRAY (2013) "The life history of *Pseudometagea schwarzii*, with a discussion of the evolution of endoparasitism and koinobiosis in Eucharitidae and Perilampidae (Chalcidoidea)," *Journal of Hymenoptera Research*, **35**, p. 1.
- [332] PÉREZ-LACHAUD, G., J. C. BARTOLO-REYES, C. M. QUIROA-MONTALVÁN, L. CRUZ-LÓPEZ, A. LENOIR, and J.-P. LACHAUD (2015) "How to escape from the host nest: Imperfect chemical mimicry in eucharitid parasitoids and exploitation of the ants' hygienic behavior," *Journal of Insect Physiology*, **75**, pp. 63–72.
- [333] AYRE, G. (1962) "*Pseudometagea schwarzii* (Ashm.) (Eucharitidae: Hymenoptera), a parasite of *Lasius neoniger* Emery (Formicidae: Hymenoptera)," *Canadian Journal of Zoology*, **40**(2), pp. 157–164.
- [334] SCHATZ, B. and J.-P. LACHAUD (2008) "Effect of high nest density on spatial relationships in two dominant ectatommine ants (Hymenoptera: Formicidae)," *Sociobiology*, **51**(3), pp. 623–644.

- [335] MANN, W. M. (1914) "Some myrmecophilous insects from Mexico," *Psyche: a Journal of Entomology*, **21**(6), pp. 171–184.
- [336] JONES, O. R., A. PURVIS, E. BAUMGART, and D. L. QUICKE (2009) "Using taxonomic revision data to estimate the geographic and taxonomic distribution of undescribed species richness in the Braconidae (Hymenoptera: Ichneumonoidea)," *Insect Conservation and Diversity*, **2**(3), pp. 204–212.
- [337] FOREL, A. (1874) *Les fourmis de la Suisse: Systématique, notices anatomiques et physiologiques, architecture, distribution géographique, nouvelles expériences et observations de moeurs*, vol. 26, Société Helvétique des Sciences Naturelles.
- [338] OLIVIER, E. (1893) *Ann. Soc. Entomol. France*, **71**.
- [339] PIERRE, A. (1893) "Un parasite des fourmis *Elasmosoma berolinense* Ruthe," *Revue Scientifique du Bourbonnais et du Centre de la France*, **6**, pp. 112–114.
- [340] WASMANN, E. (1897) *Species des Hymenopteres d'Europe et d'Algerie*, Paris, France.
- [341] DONISTHORPE, J. (1927) *British Ants*, George Routledge And Co; London, UK.
- [342] KARIYA, M. (1932) "Observations on a braconid species parasitic on ants," *Konchu Sekai*, **36**, pp. 298–301.
- [343] DURÁN, J.-M. G. and C. VAN ACHTERBERG (2011) "Oviposition behaviour of four ant parasitoids (Hymenoptera, Braconidae, Euphorinae, Neoneurini and Ichneumonidae, Hybrizontinae), with the description of three new European species," *ZooKeys*, (125), p. 59.
- [344] SHAW, S. R. (1988) "Euphorine phylogeny: the evolution of diversity in host-utilization by parasitoid wasps (Hymenoptera: Braconidae)," *Ecological Entomology*, **13**(3), pp. 323–335.
- [345] SHAW, M. and T. HUDDLESTON (1991) *Handbooks for the identification of British insects*, vol. 7, chap. Classification and biology of braconid wasps, p. 126.
- [346] SHAW, S. R. (1993) "Observations on the ovipositional behavior of *Neoneurus mantis*, an ant-associated parasitoid from Wyoming (Hymenoptera: Braconidae)," *Journal of Insect Behavior*, **6**(5), pp. 649–658.
- [347] POINAR, G. (2004) "Behaviour and development of *Elasmosoma* sp. (Neoneurinae: Braconidae: Hymenoptera), an endoparasite of *Formica* ants (Formicidae: Hymenoptera)," *Parasitology*, **128**(5), pp. 521–531.

- [348] POINAR JR, G. and J. C. MILLER (2002) "First fossil record of endoparasitism of adult ants (Formicidae: Hymenoptera) by Braconidae (Hymenoptera)," *Annals of the Entomological Society of America*, **95**(1), pp. 41–43.
- [349] YU, D. S. (1997) *Catalogue of World Ichneumonidae (Hymenoptera)*, American Entomological Institute.
- [350] KOMATSU, T. and K. KONISHI (2010) "Parasitic behaviors of two ant parasitoid wasps (Ichneumonidae: Hybrizontinae)," *Sociobiology*, **56**(3), p. 575.
- [351] MARSH, P. (1989) "Notes on the genus *Hybrizon* in North America (Hymenoptera: Paxylommatidae)," *Proceedings of the Entomological Society of Washington (USA)*.
- [352] VAN ACHTERBERG, C. (1999) "The West Palaearctic species of the subfamily Paxylommatinae (Hymenoptera: Ichneumonidae), with special reference to the genus *Hybrizon* Fallén," *Zoologische Mededeelingen*, **73**, pp. 11–26.
- [353] MASNER, L. (1993) chap. Chapter 13. Superfamily Proctotrupoidea, Research Branch Agriculture Canada Publication, Ottawa, ON, Canada, pp. pp. 537–557.
- [354] LOIACONO, M. (1987) "Un nuevo diáprido (Hymenoptera) parasitoide de larvas de *Acromyrmex ambiguus* (Emery) (Hymenoptera, Formicidae) en el Uruguay." *Revista de la Sociedad Entomologica Argentina*, **44**, pp. 129–136.
- [355] LOIÁCONO, M. S. and C. B. MARGARÍA (2000) "Systematic and cladistic analysis of the myrmecophilic genus *Gymnopria* Loiácono (Hymenoptera: Diapriidae)," *Insect Systematics & Evolution*, **31**(2), pp. 187–200.
- [356] MASNER, L. and J. L. GARCIA R (2002) "The genera of Diapriinae (Hymenoptera: Diapriidae) in the new world," *Bulletin of the American Museum of Natural History*, pp. 1–138.
- [357] LOIÁCONO, M. S., C. B. MARGARÍA, and D. A. AQUINO (2013) "Diapriinae wasps (Hymenoptera: Diaprioidea: Diapriidae) associated with ants (Hymenoptera: Formicidae) in Argentina," *Psyche: a Journal of Entomology*, **2013**.
- [358] WOJCIK, D. P. (1989) "Behavioral interactions between ants and their parasites," *Florida Entomologist*, pp. 43–51.
- [359] HUGGERT, L. and L. MASNER (1983) "Two new genera of African scelionid wasps (Hymenoptera, Proctotrupoidea: Scelionidae)," *Insect Systematics & Evolution*, **14**(2), pp. 173–185.
- [360] MAYHEW, P. J. (2007) "Why are there so many insect species? Perspectives from fossils and phylogenies," *Biological Reviews*, **82**(3), pp. 425–454.

- [361] FEENER JR, D. H. and B. V. BROWN (1997) "Diptera as parasitoids," *Annual Review of Entomology*, **42**(1), pp. 73–97.
- [362] GONZÁLEZ, C. T., W. T. WCISLO, R. CAMBRA, T. A. WHEELER, and H. FERNÁNDEZ-MARÍN (2016) "A new ectoparasitoid species of *Pseudogaurax* Malloch, 1915 (Diptera: Chloropidae), attacking the fungus-growing ant, *Apterostigma dentigerum* Wheeler, 1925 (Hymenoptera: Formicidae)," *Annals of the Entomological Society of America*, **109**(4), pp. 639–645.
- [363] FREIDBERG, A. and W. MATHIS (1985) "On the feeding habits of *Rhynchopsilopa* [Dip.: Ephydriidae]," *Entomophaga*, **30**(1), pp. 13–21.
- [364] WILLIAMS, R. and W. WHITCOMB (1974) "Parasites of fire ants in South America," in *Tall Timbers Conf. Ecol. Anim. Control Habitat Mange.*, vol. 5, pp. 49–59.
- [365] PÉREZ-LACHAUD, G., B. J. JAHYNY, G. STÄHLS, G. ROTHERAY, J. H. DELABIE, and J.-P. LACHAUD (2017) "Rediscovery and reclassification of the dipteran taxon *Nothomicrodon* Wheeler, an exclusive endoparasitoid of gyne ant larvae," *Scientific Reports*, **7**, p. 45530.
- [366] BROWN, B. V., G.-A. KUNG, and W. PORRAS (2015) "A new type of ant-decapitation in the Phoridae (Insecta: Diptera)," *Biodiversity Data Journal*, (3).
- [367] RETTENMEYER, C. W. and R. D. AKRE (1968) "Ectosymbiosis Between Phorid flies and Army ants," *Annals of the Entomological Society of America*, **61**(5), pp. 1317–1326.
- [368] BROWN, B. V., S. A. SCHNEIDER, and J. S. LAPOLLA (2011) "A new north American species of *Pseudacteon* (Diptera: Phoridae), parasitic on *Nylanderia arenivaga* (Hymenoptera: Formicidae)," *Annals of the Entomological Society of America*, **104**(1), pp. 37–38.
- [369] BROWN, B. and D. FEENER JR (1991) "Life history parameters and description of the larva of *Apocephalus paraponerae* (Diptera: Phoridae), a parasitoid of the giant tropical ant *Paraponera clavata* (Hymenoptera: Formicidae)," *Journal of Natural History*, **25**(1), pp. 221–231.
- [370] HENNE, D. and S. JOHNSON (2007) "Zombie fire ant workers: behavior controlled by decapitating fly parasitoids," *Insectes Sociaux*, **54**(2), pp. 150–153.
- [371] MORRISON, L. W. (2000) "Mechanisms of *Pseudacteon parasitoid* (Diptera: Phoridae) effects on exploitative and interference competition in host *Solenopsis ants* (Hymenoptera: Formicidae)," *Annals of the Entomological Society of America*, **93**(4), pp. 841–849.

- [372] ——— (2012) “Biological control of *Solenopsis* fire ants by *Pseudacteon* parasitoids: theory and practice,” *Psyche*, **2012**.
- [373] FOLGARAIT, P. J. (2013) “Leaf-cutter ant parasitoids: current knowledge,” *Psyche: a Journal of Entomology*, **2013**.
- [374] FOWLER, H. G. and L. F. DI ROMAGNANO (1992) “Bases ecológicas do controle biológico,” *Pesquisa Agropecuária Brasileira*, **27**(13), pp. 5–13.
- [375] BROWN, B. V. (1992) “Generic revision of Phoridae of the Nearctic Region and phylogenetic classification of Phoridae, Sciadoceridae, and Ironomyiidae (Diptera: Phoridae),” *The Memoirs of the Entomological Society of Canada*, **124**(S164), pp. 3–144.
- [376] PORTER, S. D., R. K. V. MEER, M. A. PESQUERO, S. CAMPIOLO, and H. G. FOWLER (1995) “*Solenopsis* (Hymenoptera: Formicidae) fire ant reactions to attacks of *Pseudacteon* flies (Diptera: Phoridae) in southeastern Brazil,” *Annals of the Entomological Society of America*, **88**(4), pp. 570–575.
- [377] GOSSWALD, K. (1950) “Verhandlungen der Deutschen Zoologischen Gesellschaft, Mainz 1949,” , pp. 256–264.
- [378] RETTENMEYER, C. W., M. RETTENMEYER, J. JOSEPH, and S. BERGHOFF (2011) “The largest animal association centered on one species: the army ant *Eciton burchellii* and its more than 300 associates,” *Insectes Sociaux*, **58**(3), pp. 281–292.
- [379] BARNES, J. K. (1980) “Biology and immature stages of *Helosciomyza subalpina* (Diptera: Helosciomyzidae), an ant-killing fly from New Zealand,” *New Zealand Journal of Zoology*, **7**(2), pp. 221–229.
- [380] REEMER, M. (2013) “Review and phylogenetic evaluation of associations between Microdontinae (Diptera: Syrphidae) and ants (Hymenoptera: Formicidae),” *Psyche: a Journal of Entomology*, **2013**.
- [381] PÉREZ-LACHAUD, G., M. A. JERVIS, M. REEMER, and J.-P. LACHAUD (2014) “An unusual, but not unexpected, evolutionary step taken by syrphid flies: the first record of true primary parasitoidism of ants by Microdontinae,” *Biological Journal of the Linnean Society*, **111**(2), pp. 462–472.
- [382] HOWARD, R. W., D. W. STANLEY-SAMUELSON, and R. D. AKRE (1990) “Biosynthesis and chemical mimicry of cuticular hydrocarbons from the obligate predator, *Microdon albicomatus* Novak (Diptera: Syrphidae) and its ant prey, *Myrmica incompleta* Provancher (Hymenoptera: Formicidae),” *Journal of the Kansas Entomological Society*, pp. 437–443.

- [383] HOWARD, R. W., R. D. AKRE, and W. B. GARNETT (1990) "Chemical mimicry in an obligate predator of carpenter ants (Hymenoptera: Formicidae)," *Annals of the Entomological Society of America*, **83**(3), pp. 607–616.
- [384] KATHIRITHAMBY, J. (1989) "Review of the order Strepsiptera," *Systematic Entomology*, **14**(1), pp. 41–92.
- [385] ——— (2008) *Strepsiptera*, Springer, pp. 3594–3598.
- [386] KATHIRITHAMBY, J. and S. J. TAYLOR (2005) "A new species of *Halictophagus* (Insecta: Strepsiptera: Halictophagidae) from Texas, and a checklist of Strepsiptera from the United States and Canada," *Zootaxa*, **1056**(1), pp. 1–18.
- [387] OGLOBLIN, A. A. (1939) "The Strepsiptera parasites of ants," *Int. Congr. Entomol. Berlin (1938)*, **2**, pp. 1277–1284.
- [388] KATHIRITHAMBY, J., A. HAYWARD, D. P. MCMAHON, R. S. FERREIRA, R. ANDREAZZE, H. T. D. ALMEIDA ANDRADE, and D. FRESNEAU (2010) "Conspecifics of a heterotrophic heteronomous species of Strepsiptera (Insecta) are matched by molecular characterization," *Systematic Entomology*, **35**(2), pp. 234–242.
- [389] KATHIRITHAMBY, J. and D. P. HUGHES (2002) "*Caenocholax fenyesi* (Strepsiptera: Myrmecolacidae) parasitic in *Camponotus planatus* (Hymenoptera: Formicidae) in Mexico: is this the original host?" *Annals of the Entomological Society of America*, **95**(5), pp. 558–563.
- [390] COOK, J. L. (2009) "New host association, distribution, and morphological variation in *Caenocholax fenyesi* (Strepsiptera: Myrmecolacidae)," *Proceedings of the Entomological Society of Washington*, **111**(2), pp. 370–377.
- [391] SHERMAN, P. W., T. D. SEELEY, and H. K. REEVE (1998) "Parasites, pathogens, and polyandry in honey bees," *The American Naturalist*, **151**(4), pp. 392–396.
- [392] BONAVIDA-COUGOURDAN, A., J. CLÉMENT, and C. LANGE (1987) "Nestmate recognition: the role of cuticular hydrocarbons in the ant *Camponotus vagus* Scop." *Journal of Entomological Science*, **22**(1), pp. 1–10.
- [393] MOREL, L. and R. VANDER MEER (1987) "Nestmate recognition in *Camponotus floridanus*: behavioral and chemical evidence for the role of age and social experience," *Chemistry and Biology of Social Insects*, p. 471.
- [394] GRACIA, E. S., C. DE BEKKER, E. M. HANKS, and D. P. HUGHES (2018) "Within the fortress: A specialized parasite is not discriminated against in a social insect society," *PloS One*, **13**(2), p. e0193536.
- [395] LENOIR, A., P. D'ETTORRE, C. ERRARD, and A. HEFETZ (2001) "Chemical ecology and social parasitism in ants," *Annual Review of Entomology*, **46**(1), pp. 573–599.

- [396] ELITH, J., C. H. GRAHAM, R. P. ANDERSON, M. DUDÍK, S. FERRIER, A. GUISAN, R. J. HIJMANS, F. HUETTMANN, J. R. LEATHWICK, A. LEHMANN, ET AL. (2006) “Novel methods improve prediction of species’ distributions from occurrence data,” *Ecography*, pp. 129–151.
- [397] MACARTHUR, R. H. and E. O. WILSON (1967) “The theory of island biogeography,” *Princeton, New Jersey*.
- [398] ——— (2016) *The theory of island biogeography*, Princeton University Press, Princeton, USA.
- [399] WOLFE, N. D., C. P. DUNAVAN, and J. DIAMOND (2007) “Origins of major human infectious diseases,” *Nature*, **447**(7142), pp. 279–283.
- [400] SMITH, K. F., M. GOLDBERG, S. ROSENTHAL, L. CARLSON, J. CHEN, C. CHEN, and S. RAMACHANDRAN (2014) “Global rise in human infectious disease outbreaks,” *Journal of the Royal Society Interface*, **11**(101), p. 20140950.
- [401] DWYER, G., J. DUSHOFF, and S. H. YEE (2004) “The combined effects of pathogens and predators on insect outbreaks,” *Nature*, **430**(6997), p. 341.
- [402] LEENDERTZ, F. H., H. ELLERBROK, C. BOESCH, E. COUACY-HYMAN, K. MÄTZRENSING, R. HAKENBECK, C. BERGMANN, P. ABAZA, S. JUNGLEN, Y. MOEBIUS, ET AL. (2004) “Anthrax kills wild chimpanzees in a tropical rainforest,” *Nature*, **430**(6998), p. 451.
- [403] BERMEJO, M., J. D. RODRÍGUEZ-TEIJEIRO, G. ILLERA, A. BARROSO, C. VILÀ, and P. D. WALSH (2006) “Ebola outbreak killed 5000 gorillas,” *Science*, **314**(5805), pp. 1564–1564.
- [404] CALLERI, D. V., R. B. ROSENGAUS, and J. F. TRANIELLO (2010) “Disease resistance in the drywood termite, *Incisitermes schwarzi*: Does nesting ecology affect immunocompetence?” *Journal of Insect Science*, **10**(1), p. 44.
- [405] DURRER, S. and P. SCHMID-HEMPEL (1994) “Shared use of flowers leads to horizontal pathogen transmission,” *Proceedings of the Royal Society of London B: Biological Sciences*, **258**(1353), pp. 299–302.
- [406] QUEVILLON, L. E. and D. P. HUGHES “Pathogens, parasites, and parasitoids of ants: a review and synthesis of parasite biology and host records,” .
- [407] WILSON, E. O. (1987) “Causes of ecological success: the case of the ants,” *Journal of Animal Ecology*, pp. 1–9.
- [408] HUGHES, W. O., J. EILENBERG, and J. J. BOOMSMA (2002) “Trade-offs in group living: transmission and disease resistance in leaf-cutting ants,” *Proceedings of the Royal Society of London B: Biological Sciences*, **269**(1502), pp. 1811–1819.

- [409] TRANIELLO, J. F., R. B. ROSENGAUS, and K. SAVOIE (2002) "The development of immunity in a social insect: evidence for the group facilitation of disease resistance," *Proceedings of the National Academy of Sciences*, **99**(10), pp. 6838–6842.
- [410] TARRY, D. (1969) "*Dicrocoelium dendriticum*: the life cycle in Britain," *Journal of Helminthology*, **43**(3-4), pp. 403–416.
- [411] LINDAUER, M. and B. WATKIN (1953) "Division of labour in the honeybee colony," *Bee World*, **34**(4), pp. 63–73.
- [412] MIRENDA, J. T. and S. B. VINSON (1981) "Division of labour and specification of castes in the red imported fire ant *Solenopsis invicta* Buren," *Animal Behaviour*, **29**(2), pp. 410–420.
- [413] LACHAUD, J. P. and D. FRESNEAU (1987) "Social regulation in ponerine ants," in *From individual to collective behavior in social insects: les Treilles Workshop*/edited by Jacques M. Pasteels, Jean-Louis Deneubourg, Basel: Birkhauser, 1987.
- [414] ROBINSON, G. E. (1992) "Regulation of division of labor in insect societies," *Annual Review of Entomology*, **37**(1), pp. 637–665.
- [415] KWAPICH, C. L. and W. R. TSCHINKEL (2013) "Demography, demand, death, and the seasonal allocation of labor in the Florida harvester ant (*Pogonomyrmex badius*)," *Behavioral Ecology and Sociobiology*, **67**(12), pp. 2011–2027.
- [416] BROWN, B. V. and D. H. FEENER (1998) "Parasitic phorid flies (Diptera: Phoridae) associated with army ants (Hymenoptera: Formicidae: Ecitoninae, Dorylinae) and their conservation biology," *Biotropica*, **30**(3), pp. 482–487.
- [417] PORTER, S. D., H. G. FOWLER, S. CAMPIOLO, and M. A. PESQUERO (1995) "Host specificity of several *Pseudacteon* (Diptera: Phoridae) parasites of fire ants (Hymenoptera: Formicidae) in South America," *Florida Entomologist*, pp. 70–75.
- [418] FOLGARAIT, P. J., O. A. BRUZZONE, and L. E. GILBERT (2003) "Seasonal patterns of activity among species of black fire ant parasitoid flies (Phoridae) in Argentina explained by analysis of climatic variables," *Biological Control*, **28**(3), pp. 368–378.
- [419] DUSHOFF, J., J. B. PLOTKIN, S. A. LEVIN, and D. J. EARN (2004) "Dynamical resonance can account for seasonality of influenza epidemics," *Proceedings of the National Academy of Sciences of the United States of America*, **101**(48), pp. 16915–16916.

- [420] TSCHINKEL, W. R. (1988) "Colony growth and the ontogeny of worker polymorphism in the fire ant, *Solenopsis invicta*," *Behavioral Ecology and Sociobiology*, **22**(2), pp. 103–115.
- [421] GORDON, D. M. (1996) "The organization of work in social insect colonies," *Nature*, **380**(6570), pp. 121–124.
- [422] STORK, N. E., J. MCBROOM, C. GELY, and A. J. HAMILTON (2015) "New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods," *Proceedings of the National Academy of Sciences*, **112**(24), pp. 7519–7523.
- [423] PATROCK, R. J., S. D. PORTER, L. E. GILBERT, and P. J. FOLGARAIT (2009) "Distributional patterns of *Pseudacteon* associated with the *Solenopsis saevissima* complex in South America," *Journal of Insect Science*, **9**(1), p. 60.
- [424] VALLES, S. M., D. H. OI, and S. D. PORTER (2010) "Seasonal variation and the co-occurrence of four pathogens and a group of parasites among monogyne and polygyne fire ant colonies," *Biological Control*, **54**(3), pp. 342–348.
- [425] WCISLO, W. T. (1987) "The roles of seasonality, host synchrony, and behaviour in the evolutions and distributions of nest parasites in Hymenoptera (Insecta), with special reference to bees (Apoidea)." *Biological Reviews*, **62**(4), pp. 515–542.
- [426] PÉREZ-LACHAUD, G., J. A. LÓPEZ-MÉNDEZ, and J. LACHAUD (2006) "Eucharitid parasitism of the neotropical ant *Ectatomma tuberculatum*: parasitoid co-occurrence, seasonal variation, and multiparasitism," *Biotropica*, **38**(4), pp. 574–576.
- [427] FEENER, D. H. and K. A. MOSS (1990) "Defense against parasites by hitchhikers in leaf-cutting ants: a quantitative assessment," *Behavioral Ecology and Sociobiology*, **26**(1), pp. 17–29.
- [428] FEENER JR, D. H. and B. V. BROWN (1992) "Reduced foraging of *Solenopsis geminata* (Hymenoptera: Formicidae) in the presence of parasitic *Pseudacteon* spp. (Diptera: Phoridae)," *Annals of the Entomological Society of America*, **85**(1), pp. 80–84.
- [429] FOLGARAIT, P. J. and L. E. GILBERT (1999) "Phorid parasitoids affect foraging activity of *Solenopsis richteri* under different availability of food in Argentina," *Ecological Entomology*, **24**(2), pp. 163–173.
- [430] ZIMMER, C. (2015), "More Than Half of Entire Species of Saigas Gone in Mysterious Die-Off," .

- [431] HOFFMANN, C., F. ZIMMERMANN, R. BIEK, H. KUEHL, K. NOWAK, R. MUNDRY, A. AGBOR, S. ANGEDAKIN, M. ARANDJELOVIC, and A. BLANKENBURG (2017) "Persistent anthrax as a major driver of wildlife mortality in a tropical rainforest," *Nature*, **548**(7665), pp. 82–86.
- [432] MCGLYNN, T. P., R. A. CARR, J. H. CARSON, and J. BUMA (2004) "Frequent nest relocation in the ant *Aphaenogaster araneoides*: resources, competition, and natural enemies," *Oikos*, **106**(3), pp. 611–621.
- [433] SCHMID-HEMPEL, P. and D. HEEB (1991) "Worker mortality and colony development in bumblebees, *Bombus lucorum* (L.) (Hymenoptera, Apidae)," *Mitt. Schweiz. Entomol. Ges.*, **64**, pp. 93–108.
- [434] MULLER, C. B. and P. SCHMID-HEMPEL (1992) "Correlates of reproductive success among field colonies of *Bombus lucorum*: the importance of growth and parasites," *Ecological Entomology*, **17**(4), pp. 343–353.
- [435] GORDON, D. M. (2013) "The rewards of restraint in the collective regulation of foraging by harvester ant colonies," *Nature*, **498**(7452), p. 91.
- [436] WILLIAMS, D. F., D. H. OI, S. D. PORTER, R. M. PEREIRA, and J. A. BRIANO (2003) "Biological control of imported fire ants (Hymenoptera: Formicidae)," *American Entomologist*, **49**(3), pp. 150–163.
- [437] CHOUVENC, T., N.-Y. SU, and J. K. GRACE (2011) "Fifty years of attempted biological control of termites—Analysis of a failure," *Biological Control*, **59**(2), pp. 69–82.
- [438] LORETO, R. G. and D. P. HUGHES (2016) "Disease in the society: infectious cadavers result in collapse of ant sub-colonies," *PloS One*, **11**(8), p. e0160820.
- [439] GOULSON, D., G. C. LYE, and B. DARVILL (2008) "Decline and conservation of bumble bees," *Annual Review of Entomology*, **53**, pp. 191–208.
- [440] CAMERON, S. A., J. D. LOZIER, J. P. STRANGE, J. B. KOCH, N. CORDES, L. F. SOLTER, and T. L. GRISWOLD (2011) "Patterns of widespread decline in North American bumble bees," *Proceedings of the National Academy of Sciences*, **108**(2), pp. 662–667.
- [441] GOULSON, D., E. NICHOLLS, C. BOTÍAS, and E. L. ROTHERAY (2015) "Bee declines driven by combined stress from parasites, pesticides, and lack of flowers," *Science*, **347**(6229), p. 1255957.
- [442] CHAPUISAT, M., A. OPPLIGER, P. MAGLIANO, and P. CHRISTE (2007) "Wood ants use resin to protect themselves against pathogens," *Proceedings of the Royal Society of London B: Biological Sciences*, **274**(1621), pp. 2013–2017.

- [443] DIEZ, L., P. LEJEUNE, and C. DETRAIN (2014) “Keep the nest clean: survival advantages of corpse removal in ants,” *Biology Letters*, **10**(7), p. 20140306.
- [444] PULL, C. D. and S. CREMER (2017) “Co-founding ant queens prevent disease by performing prophylactic undertaking behaviour,” *BMC Evolutionary Biology*, **17**(1), p. 219.
- [445] HART, B. L. (1990) “Behavioral adaptations to pathogens and parasites: five strategies,” *Neuroscience & Biobehavioral Reviews*, **14**(3), pp. 273–294.
- [446] KIESECKER, J. M., D. K. SKELLY, K. H. BEARD, and E. PREISSER (1999) “Behavioral reduction of infection risk,” *Proceedings of the National Academy of Sciences*, **96**(16), pp. 9165–9168.
- [447] DE ROODE, J. C. and T. LEFÈVRE (2012) “Behavioral immunity in insects,” *Insects*, **3**(3), pp. 789–820.
- [448] CURTIS, V. A. (2014) “Infection-avoidance behaviour in humans and other animals,” *Trends in Immunology*, **35**(10), pp. 457–464.
- [449] QUEVILLON, L. E., E. M. HANKS, S. BANSAL, and D. P. HUGHES (2015) “Social, spatial, and temporal organization in a complex insect society,” *Scientific Reports*, **5**, p. 13393.
- [450] LECLERC, J.-B. and C. DETRAIN (2018) “Impact of colony size on survival and sanitary strategies in fungus-infected ant colonies,” *Behavioral Ecology and Sociobiology*, **72**(1), p. 3.
- [451] VISSCHER, P. K. (1983) “The honey bee way of death: necrophoric behaviour in *Apis mellifera* colonies,” *Animal Behaviour*, **31**(4), pp. 1070–1076.
- [452] CROSLAND, M., C. LOK, T. WONG, M. SHAKARAD, and J. TRANIELLO (1997) “Division of labour in a lower termite: the majority of tasks are performed by older workers,” *Animal Behaviour*, **54**(4), pp. 999–1012.
- [453] JACCOUD, D., W. HUGHES, and C. JACKSON (1999) “The epizootiology of a *Metarhizium* infection in mini-nests of the leaf-cutting ant *Atta sexdens rubropilosa*,” *Entomologia Experimentalis et Applicata*, **93**(1), pp. 51–61.
- [454] CHOUVENC, T. and N.-Y. SU (2012) “When subterranean termites challenge the rules of fungal epizootics,” *PLoS One*, **7**(3), p. e34484.
- [455] DIEZ, L., L. URBAIN, P. LEJEUNE, and C. DETRAIN (2015) “Emergency measures: Adaptive response to pathogen intrusion in the ant nest,” *Behavioural Processes*, **116**, pp. 80–86.

- [456] GILLESPIE, D. T. (1976) “A general method for numerically simulating the stochastic time evolution of coupled chemical reactions,” *Journal of Computational Physics*, **22**(4), pp. 403–434.
- [457] R DEVELOPMENT CORE TEAM (2012) *R: A Language and Environment for Statistical Computing*, Vienna, Austria.
- [458] SAWYER, R. K. (2005) *Social emergence: Societies as complex systems*, Cambridge University Press.
- [459] BRADBURY, J. and S. VEHCAMP (2014) “Complexity and behavioral ecology,” *Behavioral Ecology*, **25**(3), pp. 435–442.
- [460] CAMAZINE, S. (2003) *Self-organization in biological systems*, Princeton University Press.
- [461] BOOMSMA, J. J. and N. R. FRANKS (2006) “Social insects: from selfish genes to self organisation and beyond,” *Trends in Ecology & Evolution*, **21**(6), pp. 303–308.
- [462] SEELEY, T. D. and S. C. BUHRMAN (1999) “Group decision making in swarms of honey bees,” *Behavioral Ecology and Sociobiology*, **45**(1), pp. 19–31.
- [463] GARNIER, S., T. MURPHY, M. LUTZ, E. HURME, S. LEBLANC, and I. D. COUZIN (2013) “Stability and responsiveness in a self-organized living architecture,” *PLoS Computational Biology*, **9**(3), p. e1002984.
- [464] WATERS, J. S. and J. H. FEWELL (2012) “Information processing in social insect networks,” *PLoS One*, **7**(7), p. e40337.
- [465] FEFFERMAN, N. and J. TRANIELLO (2008) *Social insects as models in epidemiology: establishing the foundation for an interdisciplinary approach to disease and sociality*, Harvard University Press.
- [466] WANG, D.-I. and F. MOELLER (1970) “Division of labor and queen attendance behavior of *Nosema*-infected worker honey bees,” *Journal of Economic Entomology*, **63**, pp. 1539–1541.
- [467] HART, A. G. and F. L. RATNIEKS (2002) “Waste management in the leaf-cutting ant *Atta colombica*,” *Behavioral Ecology*, **13**(2), pp. 224–231.
- [468] CREMER, S. and M. SIXT (2009) “Analogies in the evolution of individual and social immunity,” *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**(1513), pp. 129–142.
- [469] CHRISTE, P., A. OPPLIGER, F. BANCALA, G. CASTELLA, and M. CHAPUISAT (2003) “Evidence for collective medication in ants,” *Ecology Letters*, **6**(1), pp. 19–22.

- [470] BLONDER, B., T. W. WEY, A. DORNHAUS, R. JAMES, and A. SIH (2012) “Temporal dynamics and network analysis,” *Methods in Ecology and Evolution*, **3**(6), pp. 958–972.
- [471] JEANSON, R. (2012) “Long-term dynamics in proximity networks in ants,” *Animal Behaviour*, **83**(4), pp. 915–923.
- [472] OTTERSTATTER, M. C. and J. D. THOMSON (2007) “Contact networks and transmission of an intestinal pathogen in bumble bee (*textitBombus impatiens*) colonies,” *Oecologia*, **154**(2), pp. 411–421.
- [473] PINTER-WOLLMAN, N., R. WOLLMAN, A. GUETZ, S. HOLMES, and D. M. GORDON (2011) “The effect of individual variation on the structure and function of interaction networks in harvester ants,” *Journal of the Royal Society Interface*, p. rsif20110059.
- [474] BLONDER, B. and A. DORNHAUS (2011) “Time-ordered networks reveal limitations to information flow in ant colonies,” *PloS One*, **6**(5), p. e20298.
- [475] NAUG, D. (2008) “Structure of the social network and its influence on transmission dynamics in a honeybee colony,” *Behavioral Ecology and Sociobiology*, **62**(11), pp. 1719–1725.
- [476] NAUG, D. and B. SMITH (2007) “Experimentally induced change in infectious period affects transmission dynamics in a social group,” *Proceedings of the Royal Society of London B: Biological Sciences*, **274**(1606), pp. 61–65.
- [477] SENDOVA-FRANKS, A. B., R. K. HAYWARD, B. WULF, T. KLIMEK, R. JAMES, R. PLANQUÉ, N. F. BRITTON, and N. R. FRANKS (2010) “Emergency networking: famine relief in ant colonies,” *Animal Behaviour*, **79**(2), pp. 473–485.
- [478] HANSEN, L. D. and J. H. KLOTZ (2005) *Carpenter Ants of the United States and Canada*, Cornell University Press, Ithaca, NY, USA.
- [479] GORDIS, L. (2014) *Epidemiology*, 5 ed., Saunders, an imprint of Elsevier, Philadelphia, PA.
- [480] CSARDI, G. and T. NEPUSZ “The igraph software package for complex network research,” in *InterJournal, Complex Systems*, vol. 1695.
- [481] NEWMAN, M. (2010) *Networks: an introduction*, Oxford University Press.
- [482] BELL, D. C., J. S. ATKINSON, and J. W. CARLSON (1999) “Centrality measures for disease transmission networks,” *Social Networks*, **21**(1), pp. 1–21.
- [483] BURT, R. S. (2001) *Structural holes versus network closure as social capital*, Aldine de Gruyter.

- [484] BASTIAN, M., S. HEYMANN, and M. JACOMY (2009), “Gephi: An Open Source Software for Exploring and Manipulating Networks,” .
- [485] MILO, R., S. SHEN-ORR, S. ITZKOVITZ, N. KASHTAN, D. CHKLOVSKII, and U. ALON (2002) “Network motifs: simple building blocks of complex networks,” *Science*, **298**(5594), pp. 824–827.
- [486] MIHAIL, C., G. MILENA, and E. ZEGURA (2003) “The markov chain simulation method for generating connected power law random graphs,” in *Proceedings of the Fifth Workshop on Algorithm Engineering and Experiments*, vol. 111, SIAM, p. 16.
- [487] HANKS, E. M., M. B. HOOTEN, and M. W. ALLDREDGE (2012) “Continuous-Time Discrete-Space Models for Animal Movement Data,” *arXiv*.
- [488] HOOTEN, M. B., D. S. JOHNSON, E. M. HANKS, and J. H. LOWRY (2010) “Agent-based inference for animal movement and selection,” *Journal of Agricultural, Biological, and Environmental Statistics*, **15**(4), pp. 523–538.
- [489] BLONDER, B. (2014), “timeordered: Time-ordered and time-aggregated network analyses,” .
- [490] PINTER-WOLLMAN, N., E. A. HOBSON, J. E. SMITH, A. J. EDELMAN, D. SHIZUKA, S. DE SILVA, J. S. WATERS, S. D. PRAGER, T. SASAKI, G. WITTEMYER, J. FEWELL, and D. B. MCDONALD (2013) “The dynamics of animal social networks: analytical, conceptual, and theoretical advances,” *Behavioral Ecology*, **25**(2), pp. 242–255.
- [491] FERRARI, M. J., S. BANSAL, L. A. MEYERS, and O. N. BJØRNSTAD (2006) “Network frailty and the geometry of herd immunity,” *Proceedings of the Royal Society of London B: Biological Sciences*, **273**(1602), pp. 2743–2748.
- [492] KAPPELER, P. M., S. CREMER, and C. L. NUNN (2015) “Sociality and health: impacts of sociality on disease susceptibility and transmission in animal and human societies,” *Philosophical Transactions of the Royal Society of London B: Biological Sciences*.
- [493] SCHALLER, M. (2011) “The behavioural immune system and the psychology of human sociality,” *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**(1583), pp. 3418–3426.
- [494] BONDS, M. H., D. C. KEENAN, A. J. LEIDNER, and P. ROHANI (2005) “Higher disease prevalence can induce greater sociality: a game theoretic coevolutionary model,” *Evolution*, **59**(9), pp. 1859–1866.

- [495] HAGENAARS, T., C. DONNELLY, and N. FERGUSON (2004) “Spatial heterogeneity and the persistence of infectious diseases,” *Journal of Theoretical Biology*, **229**(3), pp. 349–359.
- [496] LINDHOLM, M. and T. BRITTON (2007) “Endemic persistence or disease extinction: the effect of separation into sub-communities,” *Theoretical Population Biology*, **72**(2), pp. 253–263.
- [497] RICHARDSON, T. O., J. I. LIECHTI, N. STROEYMEYT, S. BONHOEFFER, and L. KELLER (2017) “Short-term activity cycles impede information transmission in ant colonies,” *PLoS Computational Biology*, **13**(5), p. e1005527.
- [498] GERNAT, T., V. D. RAO, M. MIDDENDORF, H. DANKOWICZ, N. GOLDENFELD, and G. E. ROBINSON (2018) “Automated monitoring of behavior reveals bursty interaction patterns and rapid spreading dynamics in honeybee social networks,” *Proceedings of the National Academy of Sciences*, **115**(7), pp. 1433–1438.
- [499] CRALL, J. D., N. GRAVISH, A. M. MOUNTCASTLE, and S. A. COMBES (2015) “BEE-tag: a low-cost, image-based tracking system for the study of animal behavior and locomotion,” *PloS One*, **10**(9), p. e0136487.
- [500] BLONDER, B. (2015) *timeordered: Time-ordered and time-aggregated network analyses*.
- [501] MARTIN, S. and F. DRIJFHOUT (2009) “A review of ant cuticular hydrocarbons,” *Journal of Chemical Ecology*, **35**(10), p. 1151.
- [502] BUFFIN, A., D. DENIS, G. VAN SIMAEYS, S. GOLDMAN, and J.-L. DENEUBOURG (2009) “Feeding and stocking up: radio-labelled food reveals exchange patterns in ants,” *PloS One*, **4**(6), p. e5919.
- [503] LECLERC, J.-B. and C. DETRAIN (2017) “Loss of attraction for social cues leads to fungal-infected *Myrmica rubra* ants withdrawing from the nest,” *Animal Behaviour*, **129**, pp. 133–141.
- [504] GREENWALD, E., E. SEGRE, and O. FEINERMAN (2015) “Ant trophallactic networks: simultaneous measurement of interaction patterns and food dissemination,” *Scientific Reports*, **5**, p. 12496.
- [505] GORDON, D. M. (1995) “The development of an ant colony’s foraging range,” *Animal Behaviour*, **49**(3), pp. 649–659.
- [506] RAIMUNDO, R. L., A. V. FREITAS, and P. S. OLIVEIRA (2009) “Seasonal patterns in activity rhythm and foraging ecology in the neotropical forest-dwelling ant, *Odontomachus chelifer* (Formicidae: Ponerinae),” *Annals of the Entomological Society of America*, **102**(6), pp. 1151–1157.

- [507] FEWELL, J. H. (1988) "Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*," *Behavioral Ecology and Sociobiology*, **22**(6), pp. 401–408.
- [508] FEWELL, J. H., J. F. HARRISON, J. R. LIGHTON, and M. D. BREED (1996) "Foraging energetics of the ant, *Paraponera clavata*," *Oecologia*, **105**(4), pp. 419–427.
- [509] WEHNER, R., C. MEIER, and C. ZOLLIKOFER (2004) "The ontogeny of forage behaviour in desert ants, *Cataglyphis bicolor*," *Ecological Entomology*, **29**(2), pp. 240–250.
- [510] BEVERLY, B. D., H. MCLENDON, S. NACU, S. HOLMES, and D. M. GORDON (2009) "How site fidelity leads to individual differences in the foraging activity of harvester ants," *Behavioral Ecology*, **20**(3), pp. 633–638.
- [511] ELIZALDE, L. and P. J. FOLGARAIT (2012) "Behavioral strategies of phorid parasitoids and responses of their hosts, the leaf-cutting ants," *Journal of Insect Science*, **12**(1), p. 135.
- [512] ORR, M. R., D. L. DAHLSTEN, and W. W. BENSON (2003) "Ecological interactions among ants in the genus *Textilepithema*, their phorid parasitoids, and ant competitors," *Ecological Entomology*, **28**(2), pp. 203–210.
- [513] BRAGANCA, M. A. L., A. TONHASCA, and T. LUCIA (1998) "Reduction in the foraging activity of the leaf-cutting ant *Atta sexdens* caused by the phorid *Neodohrniphora* sp." *Entomologia Experimentalis et Applicata*, **89**(3), pp. 305–311.
- [514] ORR, M. R. and S. H. SEIKE (1998) "Parasitoids deter foraging by Argentine ants (*Textilepithema humile*) in their native habitat in Brazil," *Oecologia*, **117**(3), pp. 420–425.
- [515] LINKSVAYER, T. A., A. C. MCCALL, R. M. JENSEN, C. M. MARSHALL, J. W. MINER, and M. J. MCKONE (2002) "The function of hitchhiking behavior in the leaf-cutting ant *Atta cephalotes*," *Biotropica*, **34**(1), pp. 93–100.
- [516] OI, D. H. and R. M. PEREIRA (1993) "Ant behavior and microbial pathogens (Hymenoptera: Formicidae)," *Florida Entomologist*, pp. 63–74.
- [517] OKUNO, M., K. TSUJI, H. SATO, and K. FUJISAKI (2012) "Plasticity of grooming behavior against entomopathogenic fungus *Metarhizium anisopliae* in the ant *Lasius japonicus*," *Journal of Ethology*, **30**(1), pp. 23–27.
- [518] MODLMEIER, A. P. and S. FOITZIK (2011) "Productivity increases with variation in aggression among group members in *Temnothorax* ants," *Behavioral Ecology*, **22**(5), pp. 1026–1032.

- [519] BLIGHT, O., I. VILLALTA, X. CERDÁ, and R. BOULAY (2016) "Personality traits are associated with colony productivity in the gypsy ant *Aphaenogaster senilis*," *Behavioral Ecology and Sociobiology*, **70**(12), pp. 2203–2209.
- [520] TSCHINKEL, W. R. (2011) "Back to basics: sociometry and sociogenesis of ant societies (Hymenoptera: Formicidae)," *Myrmecological News*, **14**, pp. 49–54.
- [521] ——— (1999) "Sociometry and sociogenesis of colony-level attributes of the Florida harvester ant (Hymenoptera: Formicidae)," *Annals of the Entomological Society of America*, **92**(1), pp. 80–89.
- [522] ESPADALER, X. and S. REY (2001) "Biological constraints and colony founding in the polygynous invasive ant *Lasius neglectus* (Hymenoptera, Formicidae)," *Insectes Sociaux*, **48**(2), pp. 159–164.
- [523] BOURKE, A. F. (1991) "Queen behaviour, reproduction and egg cannibalism in multiple-queen colonies of the ant *Leptothorax acervorum*," *Animal Behaviour*, **42**(2), pp. 295–310.
- [524] LASKIS, K. O. and W. R. TSCHINKEL (2009) "The seasonal natural history of the ant, *Dolichoderus mariae*, in northern Florida," *Journal of Insect Science*, **9**(1).
- [525] HÖLLDOBLER, B. and N. F. CARLIN (1985) "Colony founding, queen dominance and oligogyny in the Australian meat ant *Iridomyrmex purpureus*," *Behavioral Ecology and Sociobiology*, **18**(1), pp. 45–58.
- [526] O'NEAL, J. and G. P. MARKIN (1975) "Brood development of the various castes of the imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae)," *Journal of the Kansas Entomological Society*, **48**, pp. 152–159.
- [527] ABRIL, S., J. OLIVERAS, and C. GÓMEZ (2010) "Effect of temperature on the development and survival of the Argentine ant, *Linepithema humile*," *Journal of Insect Science*, **10**(1).
- [528] PORTER, S. D. (1988) "Impact of temperature on colony growth and developmental rates of the ant, *Solenopsis invicta*," *Journal of Insect Physiology*, **34**(12), pp. 1127–1133.
- [529] MARKIN, G. P., H. L. COLLINS, and J. H. DILLIER (1972) "Colony founding by queens of the red imported fire ant, *Solenopsis invicta*," *Annals of the Entomological Society of America*, **65**(5), pp. 1053–1058.
- [530] ARAUJO, C. (1995) "Duration of immature stages and longevity of workers and males of *Dinoponera quadricaps* Santschi (Hymenoptera: Formicidae) in captivity." *Anais da Sociedade Entomologica do Brasil*, **24**, pp. 33–38.

- [531] KIPYATKOV, V. E. and E. B. LOPATINA (2015) "Comparative study of thermal reaction norms for development in ants," *Entomological Science*, **18**(2), pp. 174–192.
- [532] HASKINS, C. and E. HASKINS (1955) "The pattern of colony foundation in the archaic ant *Myrmecia regularis*," *Insectes Sociaux*, **2**(2), pp. 115–126.
- [533] TERRON, G. (1977) "Evolution des colonies de *Tetraoponera anthracina* Santschi (Formicidae, Pseudomyrmecinae) avec reines," *Bulletin Biologique*.
- [534] AUTUORI, M. (1956) "La fondation de sociétés chez les fourmis champignonnistes du genre "Atta"," *Fondation Singer-Polignac, L'instinct dans le comportement des animaux et de l'homme*, pp. 77–104.
- [535] ONOYAMA, K. (1981) "Brood rearing by colony founding queens of the harvester ant *Messor aciculatus*," *Japanese Journal of Entomology*, **49**(4), pp. 624–640.
- [536] WHEELER, J. and S. RISSING (1975) "Natural history of *Veromessor pergandei*. II. Behavior (Hymenoptera: Formicidae)," *Pan-Pacific Entomologist*.
- [537] KIPYATKOV, V. (1974) "Study of the photoperiodic reaction in the ant *Myrmica rubra* L. (Hymenoptera, Formicidae). I. Basic parameters of the reaction," *Entomological Review*.
- [538] PEACOCK, A. and A. BAXTER (1950) "Studies in Pharaoh's ant, *Monomorium pharaonis* (L.), 3: life history," *Entomologists' Monthly Magazine*, **86**, pp. 171–178.
- [539] ALVARES, L. E., O. BUENO, and H. FOWLER (1993) "Larval instars and immature development of a Brazilian population of pharaoh's ant, *Monomorium pharaonis* (L.) (Hym., Formicidae)," *Journal of Applied Entomology*, **116**(5), pp. 90–93.
- [540] MACKAY, W. P. (1981) "A comparison of the nest phenologies of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae)," *Psyche: a Journal of Entomology*, **88**(1-2), pp. 25–74.
- [541] BANKS, W., C. LOFGREN, D. JOUVENAZ, C. STRINGER, P. BISHOP, D. WILLIAMS, D. WOJCIK, and B. GLANCEY (1981) "Techniques for collecting, rearing, and handling imported fire ants," .
- [542] BRUDER, K. and A. GUPTA (1972) "Biology of the pavement ant, *Tetramorium caespitum* (Hymenoptera: Formicidae)," *Annals of the Entomological Society of America*, **65**(2), pp. 358–367.
- [543] NEWELL, W. (1909) "The life history of the Argentine ant," *Journal of Economic Entomology*, **2**(2), pp. 174–192.

- [544] ULLOA-CHACON, P. and D. CHERIX (1988) "Quelques aspects de la biologie de *Wasmannia auropunctata* (Roger) (Hymenoptera, Formicidae)," in *Union internationale pour l'étude des insectes sociaux. Section française. Colloque annuel*, pp. 177–184.
- [545] CONCONI, J. D., R. M. LOAEZA, J. C. AGUILAR, and G. S. ROSAS (1983) "Quelques données sur la biologie des fourmis *Liometopum* (Dolichoderinae) du Mexique et en particulier sur leurs rapports avec les homoptères," *Social insects in the tropics*, pp. 125–130.
- [546] MINTZER, A. (1979) "Foraging activity of the Mexican leafcutting ant *Atta mexicana* (F. Smith), in a sonoran desert habitat (Hymenoptera, Formicidae)," *Insectes Sociaux*, **26**(4), pp. 364–372.
- [547] BASALINGAPPA, S., V. KAREDDY, S. MATHAPATHI, and M. GANDHI (1989) "Colony-founding and life-cycle in the ant *Camponotus sericeus* Fabricius (Hymenoptera: Formicidae)," *Uttar Pradesh Journal of Zoology*, **9**, pp. 73 – 83.
- [548] SCHMIDT, G. (1974) "Steuerung der Kastenbildung und Geschlechtsregulation im Waldameisenstaat," *Sozialpolymorphismus bei Insekten. Probleme der Kastenbildung im Tierreich. Wiss. Verlagsgesellschaft, Stuttgart*, pp. 404–512.
- [549] OTTO, D. (1962) *Die Roten Waldameisen*, vol. 293, Wittenberg, Lutherstadt.
- [550] LEDOUX, A. (1950) "Recherche sur la biologie de la fourmi fileuse (*Oecophylla longinoda* Latr.)," *Ann. Sci. Nat.*, **11** - **12**(3 - 4), pp. 313 – 461.
- [551] TSCHINKEL, W. R. (1987) "Fire ant queen longevity and age: estimation by sperm depletion," *Annals of the Entomological Society of America*, **80**(2), pp. 263–266.
- [552] KRUK-DE BRUIN, M., L. C. ROST, and F. G. DRAISMA (1977) "Estimates of the number of foraging ants with the Lincoln-index method in relation to the colony size of *Formica polyctena*," *Journal of Animal Ecology*, pp. 457–470.
- [553] PORTER, S. D. and C. D. JORGENSEN (1981) "Foragers of the harvester ant, *Pogonomyrmex owyheei*: a disposable caste?" *Behavioral Ecology and Sociobiology*, **9**(4), pp. 247–256.
- [554] TSCHINKEL, W. R. (2011) "The organization of foraging in the fire ant, *Solenopsis invicta*," *Journal of Insect Science*, **11**(1), p. 26.
- [555] NOBUA-BEHRMANN, B. E., J. L. DE CASENAVE, F. A. MILESI, and B. PAVAN (2013) "Forager abundance and its relationship with colony activity level in three species of South American *Pogonomyrmex* harvester ants," *Insectes Sociaux*, **60**(2), pp. 243–249.

- [556] BROWN, M. J., A. BOT, and A. G. HART (2006) "Mortality rates and division of labor in the leaf-cutting ant, *Atta colombica*," *Journal of Insect Science*, **6**(1), p. 18.
- [557] SCHMID-HEMPEL, P. (1984) "Individually different foraging methods in the desert ant *Cataglyphis bicolor* (Hymenoptera, Formicidae)," *Behavioral Ecology and Sociobiology*, **14**(4), pp. 263–271.
- [558] GORDON, D. M. and B. HÖLLDOBLER (1987) "Worker longevity in harvester ants (*Pogonomyrmex*)," *Psyche: a Journal of Entomology*, **94**(3-4), pp. 341–346.
- [559] CALABI, P. and S. D. PORTER (1989) "Worker longevity in the fire ant *Solenopsis invicta*: ergonomic considerations of correlations between temperature, size and metabolic rates," *Journal of Insect Physiology*, **35**(8), pp. 643–649.
- [560] PORTER, S. D. and W. R. TSCHINKEL (1985) "Fire ant polymorphism: the ergonomics of brood production," *Behavioral Ecology and Sociobiology*, **16**(4), pp. 323–336.
- [561] CHAPUISAT, M. and L. KELLER (2002) "Division of labour influences the rate of ageing in weaver ant workers," *Proceedings of the Royal Society of London B: Biological Sciences*, **269**(1494), pp. 909–913.
- [562] FIELDE, A. (1904) "Tenacity of life in ants," *Biological Bulletin of the Marine Biological Laboratory, Woods Hole*, **7**(6), pp. 300–309.
- [563] PLATEAUX, L. (1986) "Comparaison des cycles saisonniers, des durees des societes et des production des trois especes de fourmis *Leptothorax* (Myrafant) du groupe nylanderii," *Actes. Coll. Ins. Soc*, **3**, pp. 221–234.
- [564] HASKINS, C. and E. HASKINS (1980) "Notes on female and worker survivorship in the archaic ant genus *Myrmecia*," *Insectes Sociaux*, **27**(4), pp. 345–350.
- [565] HARTMANN, A. and J. HEINZE (2003) "Lay eggs, live longer: division of labor and life span in a clonal ant species," *Evolution*, **57**(10), pp. 2424–2429.
- [566] DUSSUTOUR, A. and S. SIMPSON (2012) "Ant workers die young and colonies collapse when fed a high-protein diet," *Proceedings of the Royal Society of London B: Biological Sciences*, p. rspb20120051.
- [567] TSUJI, K., K. NAKATA, and J. HEINZE (1996) "Lifespan and reproduction in a queenless ant," *Naturwissenschaften*, **83**(12), pp. 577–578.
- [568] REBER, A., G. CASTELLA, P. CHRISTE, and M. CHAPUISAT (2008) "Experimentally increased group diversity improves disease resistance in an ant species," *Ecology Letters*, **11**(7), pp. 682–689.

- [569] MORRISON, L. W., C. G. DALL'AGLIO-HOLVORCEM, and L. E. GILBERT (1997) "Oviposition behavior and development of *Pseudacteon* flies (Diptera: Phoridae), parasitoids of *Solenopsis* fire ants (Hymenoptera: Formicidae)," *Environmental Entomology*, **26**(3), pp. 716–724.
- [570] PHILPOTT, S. M., I. PERFECTO, J. VANDERMEER, and S. UNO (2009) "Spatial scale and density dependence in a host parasitoid system: an arboreal ant, *Azteca instabilis*, and its *Pseudacteon* phorid parasitoid," *Environmental Entomology*, **38**(3), pp. 790–796.

Vita
LAUREN E. QUEVILLON

EDUCATION

The Pennsylvania State University	<i>anticipated August 2018</i>
Ph.D. in Biology	
Cornell University	<i>May 2010</i>
B.A. in Biology	

PUBLICATIONS

- DP Hughes, JPM Araujo, RG Loreto, **LE Quevillon**, C de Bekker, and HC Evans. 2016. From so simple a beginning: The evolution of behavioral manipulation by fungi. *Advances in genetics* 9, 437-469
- **LE Quevillon**, EM Hanks, S Bansal, and DP Hughes. 2015. Social, spatial, and temporal organization in a complex insect society. *Scientific Reports* 5, 13393
- JE Byers, AJ Malek, **LE Quevillon**, I Altman, and CL Keough. 2015. Opposing selective pressures decouple pattern and process of parasitic infection over small spatial scale. *Oikos* 124(11), 1511-1519
- C de Bekker, **LE Quevillon**, PB Smith, KR Fleming, D Ghosh, and DP Hughes. 2014. Species-specific ant brain manipulation by a specialized fungal parasite. *BMC evolutionary biology* 14(1), 166

HONORS AND AWARDS

Entomological Society of America Student Competition, Second Place	2017
<i>Systematics, Evolution, and Biodiversity Section</i>	
National Science Foundation Graduate Student Fellowship	2014 - 2017
Paul and Harriet Campbell Distinguished Graduate Fellowship	2012 - 2013
<i>The Pennsylvania State University</i>	
University Graduate Fellowship	2012 - 2013
<i>The Pennsylvania State University</i>	

TEACHING

- **Camp Director/Instructor** *Eberly College of Science Science-U* 2015 - present
- **Teaching Assistant** *The Pennsylvania State University* 2013, 2014
- **Upper School Science Instructor** *The Boys' Latin School of Maryland* 2011 - 2012
- **Chemistry Teacher** *Marianapolis Preparatory School* 2010 - 2011

SERVICE AND OUTREACH

- **President** *Center for Infectious Disease Dynamics Graduate Student Association* 2014 - 2016
- **Vice President** *Center for Infectious Disease Dynamics Graduate Student Association* 2013 - 2014
- **Keynote Speaker** *Expanding Your Horizons Science Camp* 2015
- **Invited Speaker** *Science-U Science Leadership Camp* 2015