PREVALENCE AND IMPACTS OF ANTS COLONIZING ACTIVE BIRD NESTS IN ILLINOIS

BY

JOSHUA CALEB GIBSON

THESIS

Submitted in partial fulfillment of the requirements
for the degree of Masters of Science in Entomology
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2017

Urbana, Illinois

Master's Committee:

Professor Andrew V. Suarez, Chair, Director of Research
Associate Professor Brian F. Allan
Associate Professor Michael P. Ward

ABSTRACT

Arthropod communities are often dependent on the availability of ephemeral microhabitats. Many organisms, including birds, mammals and social insects, build nests which create unique and suitable microhabitats for a variety of other animals. These constructed environments can protect their residents from predation and from harmful abiotic conditions. In turn, the communities of arthropods that colonize animal made habitats may positively or negatively influence the nest owner. Bird nests, for example, are known to harbor arthropods communities that include both harmful (e.g. ectoparasitic fly larvae) and possibly beneficial species. I quantified the arthropod communities of nests of ten species of birds in Illinois along a land-use gradient. I found workers of eight species of ants in nests, and for three of these species (*Tapinoma sessile, Temnothorax curvispinosus,* and *Crematogaster cerasi*) there was evidence that at least part of their colonies inhabited the nest. *Tapioma sessile* was the most common species and maintained the largest colonies in nest material. I found that the percentage of forest cover surrounding bird nests best predicted the presence of *T. sessile* colonies, with colonies being negatively associated with forest cover. In addition to ants, members of 19 other arthropod orders were found living in the nests. There was little evidence that ant presence influenced the abundance or prevalence of other arthropods within nests with one exception. Brown Thrasher nests with *T. sessile* colonies had fewer fly larvae and pupae than nests without ants. Fledging success did not differ between nests with and without *T. sessile* colonies for any bird species. Polydomy and a high degree of nomadism are characteristics which likely predispose ant species like *T. sessile* to colonizing active bird nests. The association between these ant species and bird nests likely is a facultative commensalism benefiting ants that is widespread in North America, and warrants further investigation.

ACKNOWLEDGEMENTS

This thesis would not have been possible without the hard work and attentiveness of Dr. Loren Merrill and members of the TJ Benson laboratory at the University of Illinois Natural History Survey, who initially noticed the presence of ants in nests they were monitoring as part of another research project. I would like to thank Danish Qazi, Reanna Kayser, Samantha Yadron Katherine Rola, Elizabeth Baehl, Jason Newton, John Lao, and Brian Rao for help sorting arthropods in the lab. I would also like to thank my advisor Dr. Andrew Suarez and my labmates Selina Ruzi, Rafael Achury, Kim Drager and Michael Rivera for providing support, constructive comments, and a good time as I worked towards completing my Master's degree. Finally, I would like to thank my adopted grandmother Isobel McCaslin for encouraging my love of insects as a child and supporting my decision to pursue entomology as a career. Issy, you are deeply missed.

TABLE OF CONTENTS

Introduction

Community composition and structure depend on the abiotic and biotic properties of the environment. Arthropod communities are particularly dependent on microhabitat availability because of their small body size and sensitivity to desiccation (Price et al. 2011). Many animals depend on "ecosystem engineers", which modify their environment and thereby create suitable microhabitats other taxa may exploit (Jones et al. 1994). Nest construction, for example, can result in structures that shelter animals from predation, and are well-buffered from environmental variation. A variety of taxa will take advantage of the conditions created by the nests of other animals. Examples include the nests and burrows of mammals, such as pack rat middens (Whitford and Steinberger 2010), and the large, often highly aggregated nests of social insects (Redford 1984; Sánchez-Piñero and Gómez 1995; Wagner et al. 1997). For some taxa, the arthropod communities that take residence in these created environments can also have large effects on the animals which created the nests.

Bird are well known for their nest building behavior and species range from creating ephemeral, single use nests, to long-lived structures that form conspicuous features on the landscape (Scott 2010). Bird nests are known to host a large diversity of arthropods (Hicks 1959; Di Iorio and Turienzo 2009). Most of these nidiculous organisms are assumed to have facultative associations with birds and their nests, but others, such as ectoparasitic fleas, ticks, nest mites and bed bugs form obligate relationships with their hosts. These parasites can have a large effect on the fitness of some bird species (Lehmann 1993) by increasing nestling mortality (Moss and Camin 1970; Brown and Brown 1986; Shields and Cook 1987; Moller 1990), premature fledging (Moss and Camin 1970; Moller 1990), and nest desertions (Duffy 1983). This is by no means the rule, however, and in many instances high parasite loads in nests appears to have no direct fitness consequences to the residents (Brown and Brown 1986; Lehmann 1993). While interactions between birds and their parasites are well studied, the ability of other nest dwelling arthropods to influence this relationship is unknown.

Ants are one of the most ecologically successful organisms and can profoundly impact the communities in which they occur (Goheen and Palmer 2009; Parr et al. 2016). Birds have evolved fascinating mutualisms with ants including “anting” behavior, where birds will either rub individual ants against their feathers or sit on top of ant mounds and let ants crawl through their feathers (Potter 1970, Revis and Waller 2004), and the army ant – ant bird foraging associations of the new world tropics (Willis and Oniki 1978, Brumfield et al. 2007). Some ants are also known to occasionally associate with bird nests. Workers of many ant species have been found in the nests of birds (Hicks 1959; Di Iorio and Turienzo 2009), and can even kill nestlings (reviewed in Suarez et al. 2005). A few species have been documented colonizing active bird nests – ants will move all or a significant portion of their colony into the nest material of bird nests (Smith 1928; Fessl et al. 2006; Gouveia et al. 2012). This interaction could affect bird fitness in a variety of ways including by influencing the arthropod communities within bird nests. Ants could decrease bird fitness by increasing rates of nestling mortality, premature fledging, and nest abandonment. Alternatively, ants could also increase fledging success by decreasing parasite load or altering the arthropod community within bird nests through predation or defensive behaviors. Many ants produce chemicals, such as formic acid, known to be antimicrobial in nature and in sufficient doses these chemicals may help to kill microbes within bird nests (Revis and Waller 2004).

I investigated the relationship between ants, bird nests, and their associated arthropod communities for 10 species of common birds in Illinois. Specifically, I addressed the following questions: 1. which species of ants colonize active bird nests; 2. how common is this interaction, and how does habitat and bird species identity influence its prevalence; 3. what ecological characteristics of ant and bird species makes them likely to participate in this interaction; and 4. how do ants influence the nest arthropod community and fledging success of birds?

Materials and Methods

Study Sites

Bird nests at ten sites around Illinois were monitored from April through July of 2014 and May through July of 2015 by Merrill et al. (2016). Information on the geographic location of each site and the species of birds examined at each is included in Table 1.

Bird Species and Nest Monitoring

Bird nests of the following species were located and marked with flagging tape placed at least 5m away from the nest: *Pipilo erythrophthalmus* (Eastern Towhee), *Dumetella carolinensis* (Gray Catbird), *Spizella pusilla* (Field Sparrow), *Cardinalis Cardinalis* (Northern Cardinal), *Toxostoma rufum* (Brown Thrasher), *Turdus migratorius* (American Robin), *Bombycilla cedrorum* (Cedar Waxwing), *Passerina caerulea* (Blue Grosbeak*), Tyrannus tyrannus* (Eastern Kingbird) and *Passerina cyanea* (Indigo Bunting). Nests were examined every three days for the presence of eggs, hatchlings and fledglings. After fledging or nest failure due to predation, nests were collected into a plastic Ziploc bag. Nest collecting occurred from June through early August in 2014 and May through July in 2015. Four additional nests in 2014 were collected in September after the nests had been abandoned. In total, 134 nests were collected and their arthropod communities surveyed. Nests were stored in a -20°C freezer until they could be examined. The approximate nest height, substrate, and fate (whether the chicks successfully fledged or not, if known) were recorded for each nest.

Land Cover Assessment

The proportion of five major land-cover types (Developed, Shrubland/Grassland, Forest, Wetland and Crop) within 500m of each nest was assessed using ArcGIS 10.2 (ESRI 2011) and Geospatial Modeling Environment (GME) (Beyer 2012). The National Agricultural Statistics Service's Cropland Data Layer (CDL) was overlaid on orthophotos for spatial reference, and to visually confirm that land use was categorized correctly (USDA NASS 2014).

Extracting Arthropods from Nests

To extract arthropods each nest was thawed and placed in a 21cm diameter sieve (W. S. Tyler Co., Cleveland OH) consisting of a 1cm mesh screen stacked on top of a 0.5cm mesh screen and separated by a height of 2cm. Nest material was pulled apart by hand and sealed inside the top of the sieve. The sieve was then vigorously shaken for 30 seconds to separate any arthropods from nest material. Material extracted from the nest was transferred to a 16.5x11.5x4.5cm plastic container and examined under a dissecting microscope. Ants were identified to species while other arthropods were identified to order and sorted to morphospecies. Specimens were then stored in 100% ethanol. Sieving was repeated five times per nest to maximize the number of arthropods extracted. An exception was American Robin nests which were only sieved once as they were densely packed with mud and contained many more arthropods (often tens of thousands per nest – most of which were mites) than feasible to sort through for this study.

Ants were identified to species using Coovert (2005) and imaged using a Leica M205 C stereo microscope (467 nm resolution) attached to a five megapixel Leica DFC 425 digital microscope camera. Bird nests were classified as possessing foragers of an ant species if one or more workers of an ant species but no queens or brood (egg, larvae and/or pupae) were found in the nest. Nest were classified as possessing an ant colony if both workers and either brood and/or queens were found.

Statistics

The prevalence of ants within nests of different bird species and different sites were compared using a test of multiple proportions (TMP). To determine which landscape level factors are important in predicting the presence of ant colonies in bird nests, a multiple logistic regression analysis was used to determine the best generalized linear model (glm) that predicted the prevalence of ants in nests. This analysis used a stepwise comparison to systematically add variables to the model (bird species, nest height, and proportion of land cover consisting of forest, crops, grassland/shrubland, wetlands, and developed areas) and calculate the corresponding improvement to the fit of the model relative to a null model using Akaike information criterion (AIC). Mean abundance of arthropod orders was compared between nests with ant colonies and nests without ant colonies using a Welsh two sample t-test for each order. All statistical analyses were performed in R version 3.3.3 (R Development Core Team).

Results

Occurrence of Ants in Bird nests

A total of eight species of ants were found in the bird nests examined in this study (Figure 1; *Tapinoma sessile, Temnothorax curvispinosus*, *Crematogaster cerasi*, *Tetramorium caespitum, Temnothorax ambiguus, Aphaenogaster fulva*, and *Formica pallidefulva*). Of these, only three (*T. sessile, T. curvispinosus*, and *C. cerasi*) were found to have colonies or parts of colonies within bird nests. *Tapinoma sessile* was the most common ant encountered, with workers present in 47 nests (35% of all nests collected), and having relatively large colony fragments living in the nest (mean ± standard deviation, number of nests: 511.29± 526.52 workers, n=31; 180± 127.63 larvae, n=25; 191.39± 183.19 pupae, n=28; 3.27± 5.99 queens, n=22). *Tapinoma sessile* was found in at least one nest of all bird species examined except Cedar Waxwing and Blue Grosbeak and occurred at nine of the ten sites included in this study. *Temnothorax curvispinosus* was the second most common ant found in nests, occurring in 25 nests (18.6% of total) of all species of birds examined except for Cedar Waxwing, Eastern Kingbird and Indigo Bunting. Occasionally, small colonies of *T. curvispinosus* were found within nests of Brown Thrasher, Eastern Towhee, Gray Catbird and Northern Cardinal (16± 10.08 workers, n=6; 2.67± 1.53 larvae, n=3; 5.17± 6.82 pupae, n=6; 1± 0 queens, n=2). *Crematogaster cerasi*, had foragers in 20 nests (14.9% of total) of all birds except Blue Grosbeak, Eastern Towhee and Indigo Bunting. However, evidence of colonies were only found in two American Robin nests. Colony size could not be accurately approximated for this species due to the sorting method used for American Robin nests, but both colonies had greater than 50 workers and brood. The other species of ants found (*Aphaenogaster fulva*, *Formica pallidefulva*, *Lasius alienus*, *Temnothorax ambiguus*, and *Tetramorium caespitum*) were only pulled from a handful of nests as small groups of workers (less than 30 individuals and usually only one or two) which likely were foragers. In many instances, workers of two or three species of ants were found in a single nest, and in one Brown Thrasher nest, both a colony of *T. sessile* and a colony of *T. curvispinosus* were found. Occurrence data on the species of ants found within bird nests in this study are summarized in Table 2.

Prevalence of Ant Colonies by Bird Species and by Site

The prevalence of *T. sessile* colonies in nests varied among bird species (Figure 2A, TMP, χ^2=21.7, df=5, p<0.001) and sites (Figure 3A, TMP, χ^2=21.1, df=5, p<0.001). However, the presence of *T. sessile* workers varied by bird species (Figure 2A, TMP, χ^2=15.4, df=5, p=0.009) but not by site (Figure 3A, TMP, χ^2=9.7, df=5, p=0.083). Similarly, the prevalence of *T. curvispinosus* colonies varied with bird species (Figure 2B, TMP, χ^2=14.1, df=5, p=0.015) as did the prevalence of workers (Figure 2B, TMP, χ^2=14.9, df=5, p=0.011). However, the prevalence of *T. curvispinosus* colonies did not vary by site (Figure 3B, TMP, χ^2=5.0, df=5, p=0.411), while worker prevalence did (Figure 3B, TMP, χ^2=11.7, df=5, p=0.039). In contrast, the prevalence of *C. cerasi* colonies did not differ between nests of different bird species (Figure 2C, TMP, χ^2=3.2, df=5, p=0.66), nor did the prevalence of foraging workers differ (Figure 2C, TMP, χ^2=3.5, df=5, p=0.62). Prevalence of *C. cerasi* colonies did vary by site (Figure 3C, TMP, χ^2=21.1, df=5, p<0.001) but prevalence of *C. cerasi* workers did not (Figure 3C, TMP, χ^2=9.7, df=5, p=0.08).

Factors Predicting Ant Prevalence

Results of the generalized linear model show that proportion of landscape covered in forest and grassland/shrubland within 500m are the best predictors of the presence of *T. sessile* colonies in bird nests (Table 3); adding bird species or proportion of land covered in developed areas, crops or wetlands did not significantly improve the prediction power of the model. This model explains between 30% and 47% of variance observed in *T. sessile* colony prevalence (Table 4).

Impact on Nidiculous Arthropod Communities and Fledging Success

Overall arthropod communities in the bird nests examined were highly variable in the number and diversity of arthropods present (Figure 4). Arthropod abundance was lower in Brown Thrasher nests containing *T. sessile* colonies (Welsh two sample t-test, t=-2.7, df=8.5, p=0.026), but not in Northern Cardinal (Welsh two sample t-test, t=0.27, df=9.2, p=0.79) or Gray Catbird nests (Welsh two sample t-test, t=-0.1, df=10.9, p=0.93). Field Sparrow and Eastern Towhee nests were excluded from these analyses due to small sample sizes for nests with and without *T. sessile* colonies. At the ordinal level, flies were significantly less abundant in Brown Thrasher nests with *T. sessile* colonies compared to those without (Figure 4A, Welsh two sample t-test, t=-3.6, df=6.2, p=0.01). No other order was significantly different in abundance between nests with and without *T. sessile* colonies in Brown Thrasher, Northern Cardinal or Gray Catbird nests (Figure 4A, B, C). The presence of *T. sessile* colonies did not have a detectable effect on fledging success of nestlings in American Robin, Northern Cardinal, Gray Catbird, Field Sparrow, Eastern Towhee or Brown Thrasher nests (Figure 5, Fisher's exact test, p>0.05).

Discussion

I investigated a long recognized but poorly understood association of birds and ants: the colonization of active bird nests by ants (Smith 1928). I found workers from eight species of ants in the nests of 10 species of birds in Illinois. Notably, three ant species (*Tapinoma sessile*, *Temnothorax curvispinosus*, and *Crematogaster cerasi*) appeared to colonize bird nests by moving at least part of their colonies into the physical structure of the nest. Of these *T. sessile* was by far the most prevalent and had the largest colonies (as many as 2000 workers and 30 queens in a single nest).

Ants and birds are known to interact in numerous ways including co-habitation which may be commensal or mutualistic. For example, the Rufous-Naped Wren will preferentially construct nests in Acacia trees that possess colonies of stinging ants of the genus *Pseudomyrmex* which will aggressively defend the tree. Presumably the birds benefit from the behavior of the ants as a form of defense for the bird’s nest (Young et al. 1990). These associations appear to be largely restricted to tropical regions, likely because of the absence of tightly linked ant-plant defensive mutualisms in temperate regions (Hölldobler and Wilson 1990).

Tapinoma sessile has been known to colonize bird nests since at least 1928. In his master’s thesis on the biology of *T. sessile*, Marion Smith mentions in passing that this species of ant was discovered nesting in bird nests by Essig (presumably Edward Olivar Essig, a prominent American entomologist). Unfortunately, the species of bird, the location of the observation, and number of occurrences are not mentioned (Smith 1928). *Tapinoma sessile* is a highly polydomous and polygynous ant, forming multiple interconnected colonies with as many as 10,000 workers and 200 queens and often relocating nests many times over the course of a season (Buczkowski and Bennett 2008; Smith 1928). Subsequently, this species may frequently move parts of its colony into sites with favorable conditions, such as protection provided by the physical structure of bird nests or the elevated temperatures provides by the presence of eggs and brooding parents. In fact, even a small increase from ambient temperature may speed up developmental times of ant larvae (Hartley and Lester 2003; Porter 1988) which is why many species will move the location of their brood within their nests throughout the day in response to local changes in temperature (Cole 1994). *Tapinoma sessile* workers develop from eggs to adults in as little as 32 days, with faster development times during warmer parts of the year (Smith 1928). Nesting duration (number of days from the start of egg incubation to fledging of chicks) for the six most common bird species examined in this study ranges from a minimum of 15 days in Field Sparrows to a maximum of 27 days in American Robins and Brown Thrashers, averaging 22.25 days across all species (Allaboutbirds.org). Assuming colonization of bird nests early in their construction, ant larvae within bird nests are able to spend half to a third of their larval/pupal lifespan in a relatively homeothermic environment above ambient temperature, likely decreasing development time significantly.

I found that the prevalence of *T. sessile* within nests among sites decreased with increasing forest cover. This relationship may be partially explained by a decrease in possible nesting locations for *T. sessile* colonies with decreasing forest and shrub cover, making bird nests more appealing. *Tapinoma sessile* is known to live in a variety of habitat types, including urban environments, but is particularly common in forests in central Illinois (Belcher et al. 2016). Collecting data on habitat structure at a smaller spatial scale and examining the relative abundance of *T. sessile* colonies nesting in places other than bird nests at each site might shed more light on this subject. I did not collect data relevant to at what stage of nest construction ants move into bird nests, or for how long they remain after the nests have been abandoned, but the highly nomadic habits of this species and their tendency to abandon nest locations for nests in more suitable substrates in as little as 21 days after first inhabiting a nest site (Meissner and Silverman 2001; Smallwood and Culver 1979) warrants the investigation of this aspect of the relationship in a future study.

The second most common ant encountered was *T. curvispinosus*. *Temnothorax curvispinosus* is an “acorn ant”, forming small colonies (typically 80-100 workers) within hollowed out twigs or acorns on the forest floor, and is also highly nomadic, polydomous and polygynous (Coovert 2005). The appearance of *T. curvispinosus* colonies in bird nests is a bit surprising considering its reputation as a litter dwelling species. However, *T. curvispinosus* workers are known to forage semi-arboreally, sometimes appearing at the extrafloral nectaries of bigtooth aspen (Davis and Bequaert 1922). It is possible that above ground nesting in this species is simply overlooked or not reported. Alternatively, as all of the bird species with which *T. curvispinosus* were found to associate incorporate many sticks and twigs into their nests, it’s possible that these colonies are subsets of larger colonies that were accidentally moved into birds’ nests through the transport of nest construction material. The smaller than average colony sizes detected in this study might be explained by this method of inoculation. Detailed monitoring of bird nests over the course of their formation for *T. curvispinosus* colonies is needed to determine if this is possible, although the small colony and body size of this species would make them difficult to detect without major disturbance to bird nests. There likely is little or no competition between *T. curvispinosus* and *T. sessile* colonies for space in bird nests, as evident by the co-occurrence of colonies of both species in one Brown Thrasher nest.

Crematogaster cerasi was the least commonly encountered ant found colonizing bird nests in this study, although many nests had a relatively high number of workers in them (as many as 200). *Crematogaster cerasi* is a relatively common forest dwelling ant in the Midwest and normally nests under stones or decaying logs, although nests found inside hollow stems or human-made objects are not uncommon (Coovert 2005). The semi-arboreal foraging and generalized dietary habits of this species may explain their frequency of occurrence in bird nests, but little of the biology of this species is known compared to the other two commonly encountered species in this study.

The nesting habits of these ants may help inform what characteristics allow them to utilize bird nests as a nesting resource. All species of ants found colonizing bird nests in this study are opportunistic in their nesting habits, occupying found spaces which they modify very little (Coovert 2005; Smith 1928). Both *T. sessile* and *T. curvispinosus* are nomadic and polydomous, allowing them to exploit temporary nesting resources (Coovert 2005; Hölldobler and Wilson 1990; Smith 1928). Both also have either lost their stinger (*T. sessile*) or lack the ability to sting vertebrates (*T. curvispinosus*), so they likely are easily tolerated by birds. Together, these behaviors likely make these species preadapted to utilizing bird nests as a nesting source. It is unknown if the ants obtain any other benefits from this association, but the thermal stability and higher relative temperatures of active bird nests might improve the development time of larval *T. sessile* as has been shown in other species of ants (Hartley and Lester 2003; Porter 1988).

The arthropod communities in the bird nests examined in this study were highly variable in terms of the taxa and number of arthropods but consistent with groups known to occur in bird nests (Hicks 1959). Many of these groups, such as thrips, isopods, and spiders likely are associating with bird nests facultatively, exploiting the temporary microhabitat created by birds in a similar fashion to the ant species described above. Others, such as flies and nest mites, are likely associating with bird nests obligately as ectoparasites. Many ectoparasitic groups expected to be found in high abundance within nests, such as fleas and lice, were only collected in small numbers from a few nests or not at all. These taxa are likely so closely associated with their hosts that they leave nests quickly after they have been abandoned by the birds. I found significantly fewer fly larvae and pupae in Brown Thrasher nests with *T. sessile* colonies compared to those without. However, this reduction was not found for other bird species, and no other arthropod order in either Brown Thrasher, Northern Cardinal or Gray Catbird nests differed significantly between nests with colonies and nests without. This suggests that while *T. sessile* colonies have the potential to influence the composition of arthropod communities in bird nests, this effect may be restricted to certain taxa. Although not identified to species, the majority of fly larvae found in these nests likely were ectoparasitic blow flies which are known to significantly impact the health of nestlings in some species of birds via exsanguination (Lehmann 1993). Why *T. sessile*'s effect on fly abundance is restricted to Brown Thrasher nests is unknown, but could be due to with the specific biology of the fly species associated with Brown Thrashers or differences in nest construction between bird species. The ability of ants to reduce fly abundance in bird nests may be widespread; in nests of Galapagos finches the introduced ectoparasitic fly *Philornis downsi* appears to be reduced in abundance when *Camponotus* ants colonize nests (Fessl et al. 2006).

In Brown Thrasher nests the reduction of fly abundance associated with the presence of *T. sessile* colonies does not appear to affect the fledging success of nestlings as there was no difference in fledging rates between Brown Thrasher nests with or without *T. sessile* colonies. Likewise, no other species of bird was found to have differential fledging success rates in nests with *T. sessile* colonies compared to those without. Thus *T. sessile* likely is a tolerated facultative commensalist in bird nests, although any effects *T. sessile* could have on fledging success may be either minor and undetectable with the relatively small sample sizes used in this study, or delayed and only apparent after fledging has occurred.

This association between ants and bird nests appears to be quite common in Illinois, involving multiple species of ants and birds. Since the behaviors that may facilitate this interaction in ants (polydomy and nomadism) are present in many more ant taxa than were discovered here, more species of ants likely participate in this association and could have significant effects on the nesting biology of birds. Future studies should expand this research to include more bird species and different geographic locations in the hopes of determining the true extent of this association. A more focused study on a single ant-bird nest interaction, such as *T. sessile* and Brown Thrashers, also is needed to increase our understanding of the positive, negative or neutral effects each species involved could receive.

Tables and Figures

Table 1. Geographic locations for all sites included in this study and the species of birds that were collected at each. All coordinates are ± 1km. AMRO: American Robin, BLGR: Blue Grosbeak, BRTH: Brown Thrasher, CEDW: Cedar Waxwing, EAKI: Eastern Kingbird, EATO: Eastern Towhee, FISP: Field Sparrow, GRCA: Gray Catbird, INBU: Indigo Bunting, NOCA: Northern Cardinal.

Site	Abbreviation	Latitude (°N)	Longitude (°W)	Bird Species Present (number of nests)
University of Illinois Pollinatarium	POLLI	40° 5'5.66"	88°12'58.65"	AMRO (13), BRTH (7), GRCA (6), NOCA (4)
Vermillion River Observatory	VRO	40° 3'29.28"	87°33'47.22"	AMRO (7), BRTH (2), EATO (4), FISP (10), GRCA (4), INBU (1), NOCA (4)
Middlefork River Forest Preserve	MFRFP	40°22'27.34"	87°57'19.08"	AMRO (7), FISP (6), NOCA (3)
Grein Farm	GREIN	40° 5'1.71"	88°13'25.96"	AMRO (5), GRCA (1)
Lake of the Woods Forest Preserve	LOTW	40°12'16.12"	88°13'25.96"	AMRO (1), BLGR (1), CEDW (1), EAKI (1), FISP (1), NOCA (5)
Kennekuk County Park	KCP	40°11'36.76"	87°41'55.92"	AMRO (1), BRTH (4), EATO (5), FISP (1), GRCA (2), NOCA (3)
Abandoned dump site in Urbana IL	DUMP	40° 7'25.36"	88°11'6.58"	AMRO (6), BRTH (1), FISP (1), GRCA (3)
Green Valley Forest Preserve	GVFP	41°44'22.56"	88° 4'30.97"	AMRO (2), BRTH (1), GRCA (1)
Morraine Hills State Park	MHSP	42°18'53.33"	88°13'55.65"	BRTH (1)
Herrick Lake Forest Preserve	HLFP	41°49'8.80"	88° 7'47.40"	GRCA (2)

Table 2. Summary of ant occurance in bird nests of central and northern Illinois. W designates some nests of a bird speceis have been found with workers only of a given ant species, C designates that colonies of the given ant species have been found in at least one nest, and A indicates only an alate queen was found. DUMP - abandoned dump site in Urbana, HLFP - Herrick Lake Forest Preserve, GREIN - Grein Farm, GVFP - Green Valley Forest Preserve, KCP - Kennekuk County Park, LOTW - Lake of the Woods Forest Preserve, MFRFP - Middlefork River Forest Preserve, MHSP - Morraine Hills State Park, POLLI - University of Illinois Pollinatarium, VRO - Vermillion River Observatory, AMRO - American Robin, BLGR - Blue Grosbeak, BRTH - Brown Thrasher, CEDW - Cedar Waxwing, EAKI - Eastern Kingbird, EATO - Eastern Towhee, FISP - Field Sparrow, INBU - Indigo Bunting, NOCA - Northern Cardinal.

Ant Species	Field Sites	AMRO	BLGR	BRTH	CEDW	EAKI	EATO	FISP	GRCA	INBU	NOCA
Aphaenogaster fulva	KCP			W							
Crematogaster cerasi	DUMP, GREIN, GVFP, KCP, LOTW, MFRFP, POLLI	C, W		W	W	W		W	W		W
Formica pallidefulva	VRO							W			
Lasius alienus	MFRFP, VRO	W									
Tapinoma sessile	DUMP, HLFP, GVFP, KCP, LOTW, MFRFP, MHSP, POLLI, VRO	C, W		C		C	C	W, C	W, C	C	W, C
Temnothorax ambiguus	MFRFP							W			
Temnothorax curvispinosus	DUMP, KCP, LOTW, MFRFP, POLLI, VRO	W	W	W, C			W, C	W	W, C		A, W, C
Tetramorium caespitum	POLLI			W					W		W

Table 3. Analysis of maximum likelihood estimates for the best fit generalized linear model resulting from a multiple linear regression analysis to determine habitat factors predicting the presence of ants in bird nests. Forest and grassland/shrubland represent the proportion of land within 500m of each nest covered in that habitat type.

Analysis of Maximum Likelihood Estimates					
Parameter	DF	Estimate	Standard Error	z value	Pr >z
Intercept	1	2.0629	0.5835	3.536	0.0004
Forest	1	-3.1332	1.1354	-2.76	0.0057
Grassland/ Shrubland	1	-0.9754	1.5601	-0.625	0.5318

Table 4. Pseudo-R^2 values for the generalized linear model predicting the presence of ants in bird nests.

Pseudo-R^2 type	Pseudo-R^2 value
McFadden	0.30
Cox and Snell (ML)	0.38
Nagelkerke (Cragg and Uhler)	0.47

Figure 1. Representative specimens of each species of ant found in this study. A – *Tapinoma sessile*, B – *Temnothorax curvispinosus*, C – *Crematogaster cerasi*, D – *Tetramorium caespitum*, E – *Temnothorax ambiguous*, F – *Aphaenogaster fulva*, G – *Formica pallidefulva*., H – *Lasius alienus*. All images taken by the author.

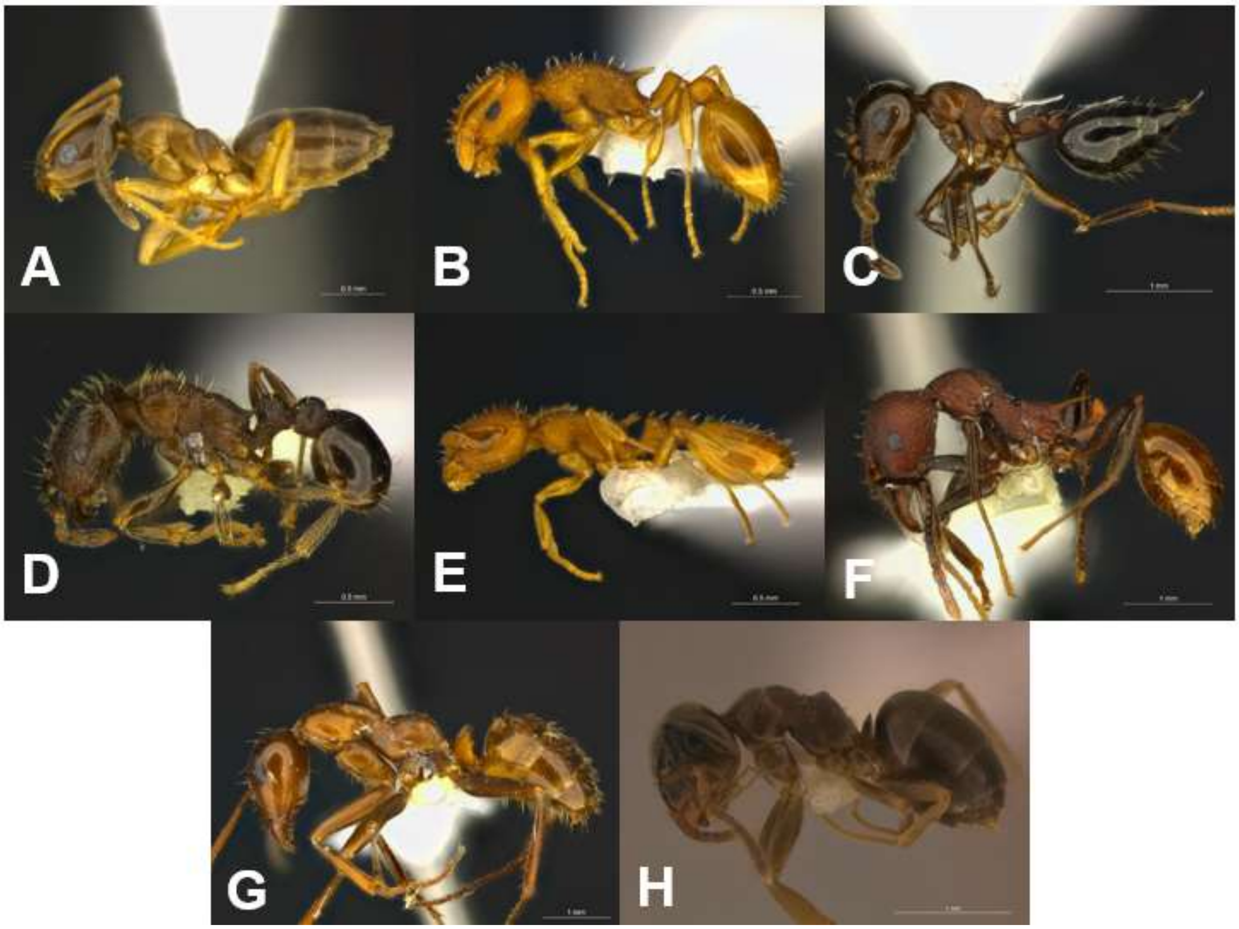


Figure 2. Prevalence of ants in nests of the six most abundantly surveyed birds in this study. Values are given as a proportion of the total number of nests. Asterisks denote groups that significantly differ between bird species when compared using a test of equal proportions. Numbers at the bottom of each bar represent the total number of nests examined per species. Black bars represent proportion of nests containing colonies, Gray bars represent proportion of nests containing foraging workers. A: *Tapinoma sessile*, B: *Temnothorax curvispinosus*; C: *Crematogaster cerasi*. AMRO – American Robin, BRTH – Brown Thrasher, EATO – Eastern Towhee, FISP – Field Sparrow, GRCA – Gray Catbird, NOCA – Northern Cardinal. Pictures used with permission from Alex Wild photography.

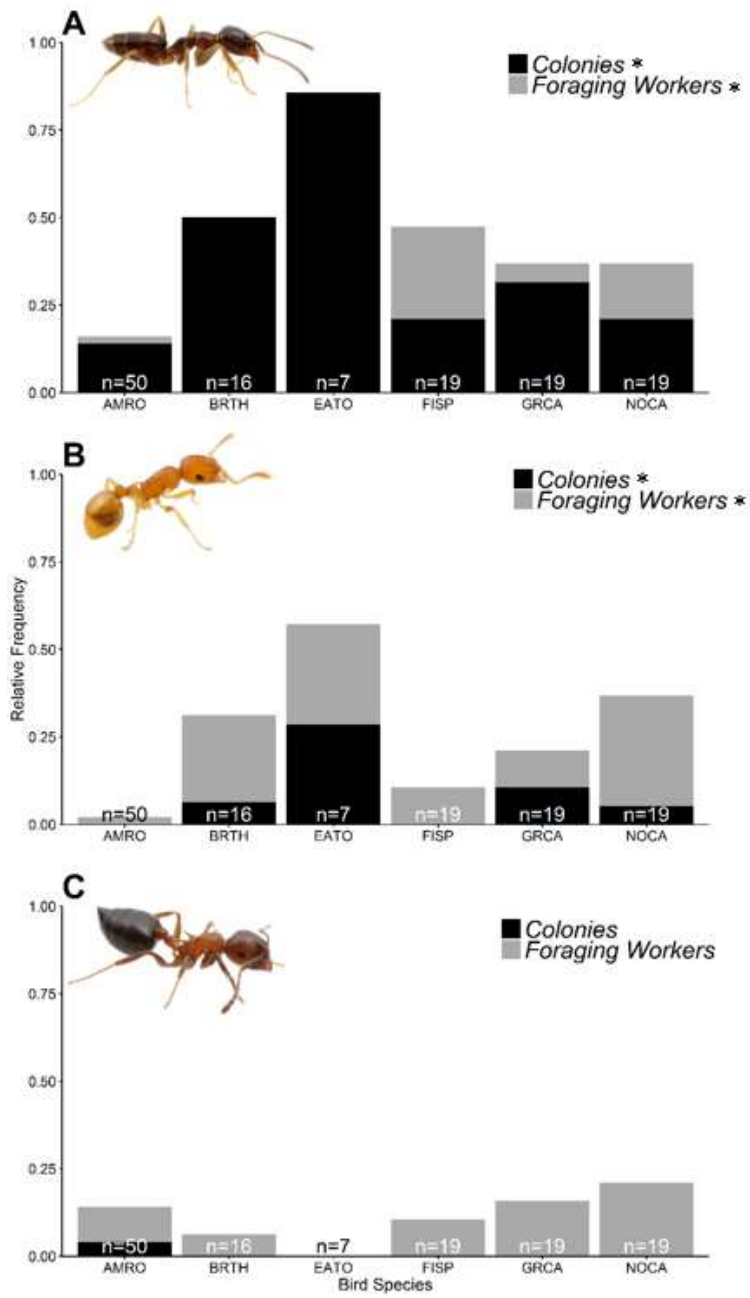


Figure 3. Prevalence of ants in nests of at different Field sites used in this study. Only sites where more than 10 nests were collected are shown. Values are given as a proportion of the total number of nests. Asterisks denote groups that significantly differ between sites when compared using a test of equal proportions. Numbers at the bottom of each bar represent the total number of nests examined per site. Black bars represent proportion of nests containing colonies, Gray bars represent proportion of nests containing foraging workers. A: *Tapinoma sessile*, B: *Temnothorax curvispinosus*; C: *Crematogaster cerasi*. DUMP: abandoned dump site in Urbana IL, KCP: Kennekuk County Park, LOTW: Lake of the Woods Forest Preserve, MFRFP: Middlefork River Forest Preserve, POLLI: University of Illinois Pollinatarium, VRO: Vermillion River Observatory. Pictures used with permission from Alex Wild photography.

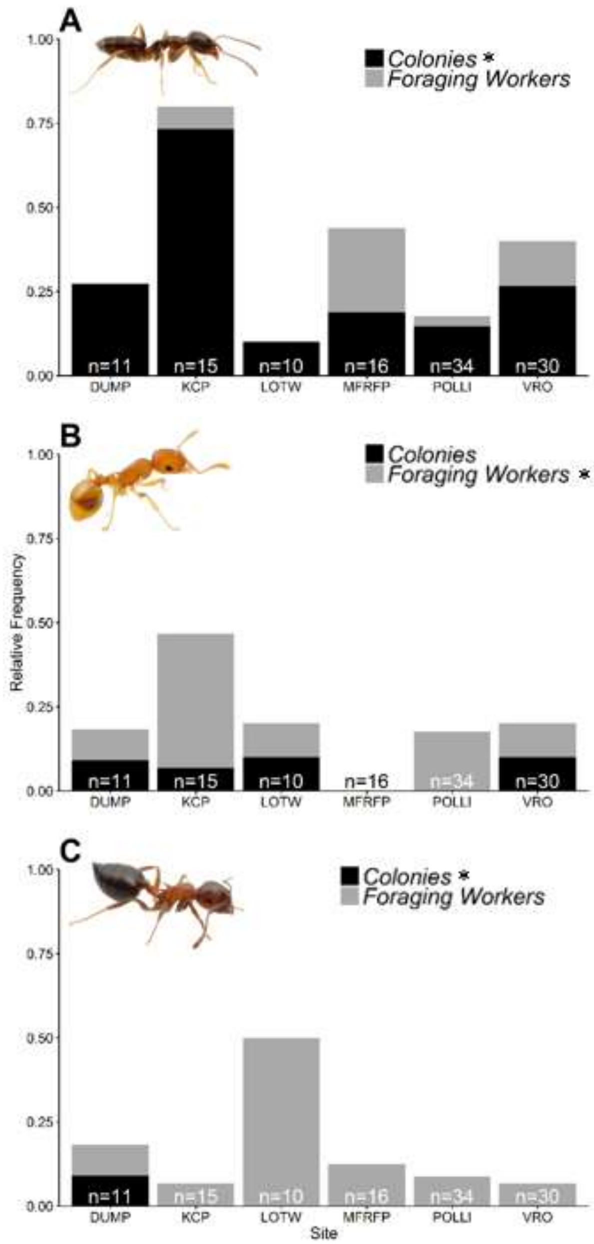


Figure 4. Mean abundance of arthropod orders in nests with and without *T. sessile* colonies. Asterisks denote orders which are significantly lower in abundance in nests with colonies compared to nests without colonies (Welsh two sample t-test, $p<0.05$). Error bars represent one standard deviation from the mean; bars lacking error bars have standard deviations greater than their mean. A: Brown Thrasher nests, B: Gray Catbird nests, C: Northern Cardinal nests.

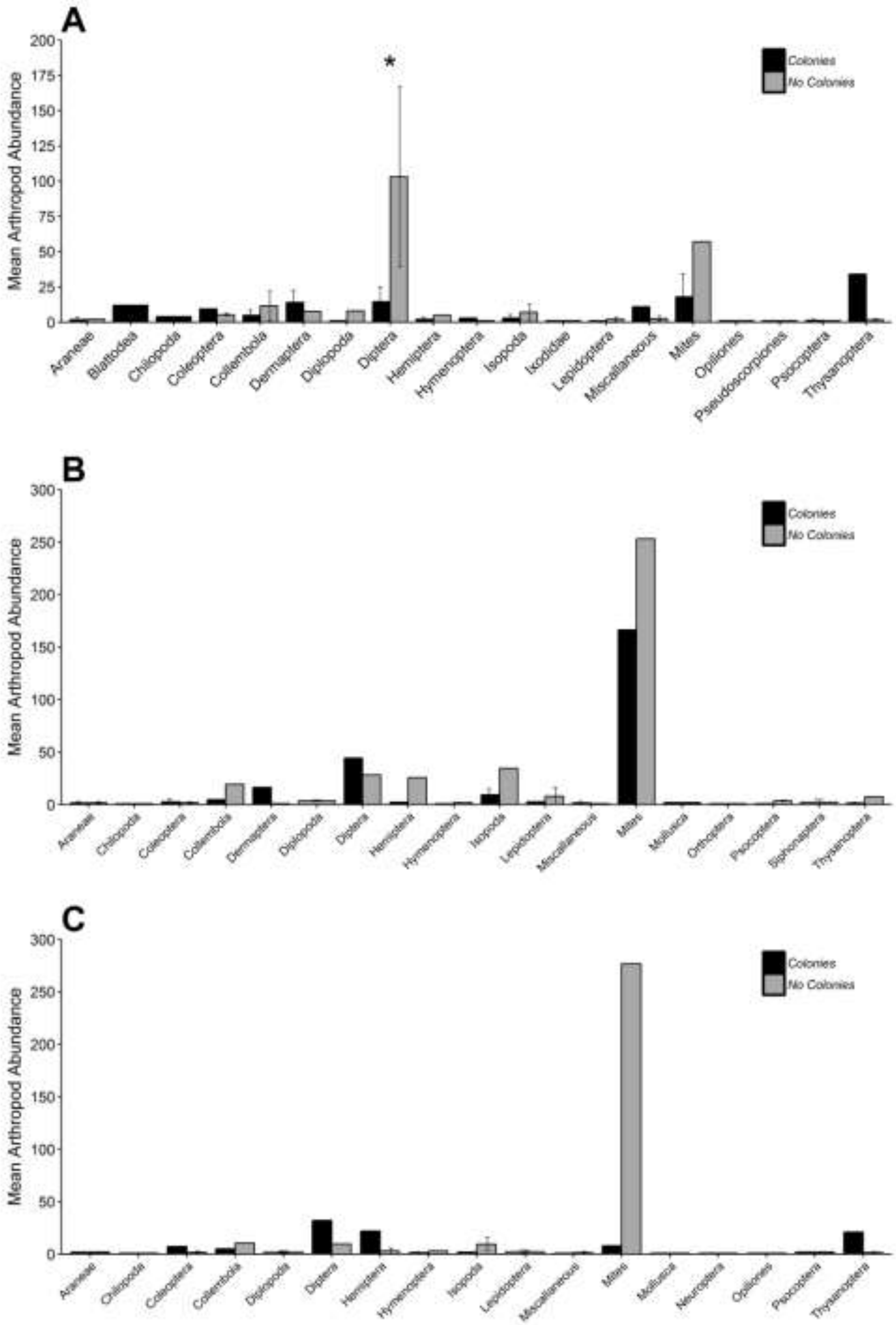
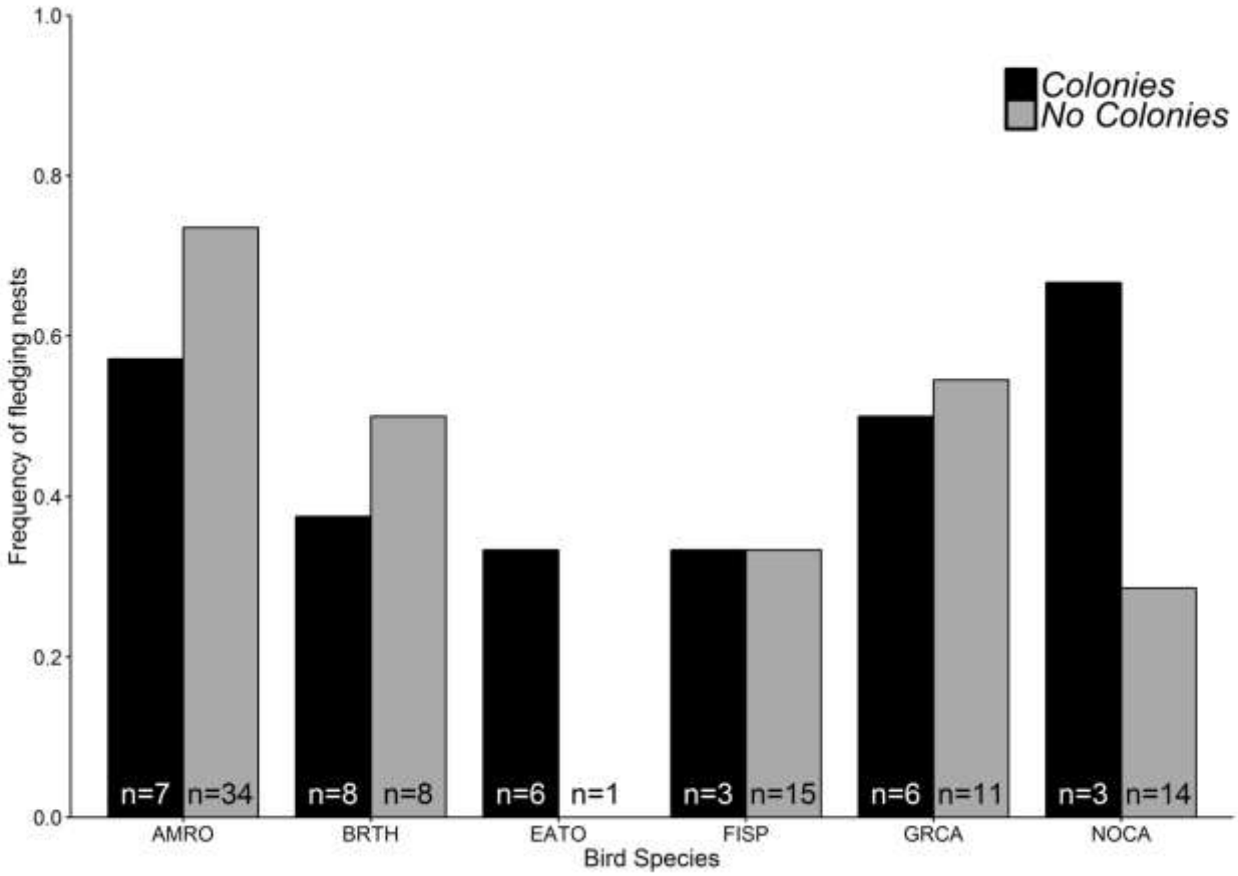


Figure 5. Frequency of nests that had at least one fledgling from nests that contain *T. sessile* colonies versus nests that do not for the six most abundant bird species examined. Frequencies within species are not significantly different between nests with colonies and nests without colonies (Fisher's exact test, p>0.05). AMRO – American Robin, BRTH – Brown Thrasher, EATO – Eastern Towhee, FISP – Field Sparrow, GRCA – Gray Catbird, NOCA – Northern Cardinal.



References

Belcher, A.K., M.R. Berenbaum, and A.V. Suarez. 2016. Urbana house ants 2.0: Revisiting M. R. Smith's 1926 survey of house-infesting ants in central Illinois after 87 years. *American Entomologist* 62: 182-193.

Brown, C.R., and M.B. Brown. 1986. Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). *Ecology* 67: 1206-1218.

Brumfield, R.T., J.G. Tello, Z.A. Cheviron, M.D. Carling, N. Crochet, and K.V. Rosenberg. 2007. Phylogenetic conservatism and antiquity of a tropical specialization: Army-ant-following in the typical antbirds (Thamnophilidae). *Molecular Phylogenetics and Evolution* 45: 1-13.

Buczkowski, G., and G. Bennett. 2008. Seasonal polydomy in a polygynous supercolony of the odorous house ant, *Tapinoma sessile*. *Ecological Entomology* 33: 780-788.

Cole, B.J. 1994. Nest architecture in the western harvester ant, *Pogonomyrmex occidentalis* (Cresson). *Insectes Sociaux* 41: 401-410.

Coovert, G.A. 2005. The ants of Ohio. *Bulletin of the Ohio Biological Survey* 15(2): 1-196.

Cornell Lab of Ornithology. *All About Birds*. www.allaboutbirds.org. Accessed 17 April 2017.

Davis, W.T., and J. Bequaert. 1922. An annotate list of the ants of Staten Island and Long Island N.Y. *Bulletin of the Brooklyn Entomological Society* 17:1-25.

Di Iorio, O., and P. Turienzo. 2009. Insects found in birds' nests from the Neotropical region (except Argentina) and immigrant species of Neotropical origin in the Nearctic region. *Zootaxa* 2187: 1-144.

Duffy, D.C. 1983. The ecology of tick parasitism on densely nesting Peruvian seabirds. *Ecology* 64: 110-119.

Fessl, B., S. Kleindorfer, and S. Tebbich. 2006. An experimental study on the effects of an introduced parasite in Darwin's finches. *Biological Conservation* 127: 55-61.

Goheen, J.R., and T.M. Palmer. 2009. Defensive plant-ants sabilive megahervibore-driven landscape change in an African savanna. *Current Biology* 20: 1768-1772.

Gouveia, F.B.P., M.L.L. Barbosa, and T.V. Barrett. 2012. Arthropods associated with nests of *Cacicus* sp. and *Psarocolius* sp. (Passerida: Icteridae) in varzea forest near the meeting of the rivers Negro and Solimões (Central Amazonia: Brazil) at high water. *Journal of Natural History* 46: 979-1003.

Hansell, M. 2000. *Bird Nests and Construction Behavior*. New York: Cambridge University Press.

Hartley, S., and P.J. Lester. 2003. Temperature-dependent development of the Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae): A degree-day model with implications for range limits in New Zealand. *New Zealand Entomologist* 26: 91-100.

Hicks, E.A. 1959. *Check-list and bibliography on the occurrence of insects in bird´ nests.* Ames: Iowa State College Press.

Hölldobler, B., and E.O. Wilson. 1990. *The Ants*. Cambridge: Belknap Press.

Jones, C.G., J.H. Lawton, and M. Shachak. Organisms as ecosystem engineers. *Oikos* 69: 373-386.

Lehmann, T. 1993. Ectoparasites: Direct impact on host fitness. *Parasitology Today* 9: 8-13.

Meissner, H.E., and J. Silverman. 2001. Effects of aromatic Cedar mulch on the Argentine ant and the odorous house ant (Hymenoptera: Formicidae). *Journal of Economic Entomology* 94: 1526-1531.

Merrill, L., E.M. Baehl, K.E. Ripple, and T.J. Benson. 2016. Do birds alter their levels of parental investment based on nest-site habitat features? *Ethology* 122: 1-10.

Moller, A.P. 1990. Effects of parasitism by haematophagous mite on reproduction in the barn swallow. *Ecology* 71: 2345-2357.

Moss, W.W., and J.H. Camin. 1970. Nest parasitism, productivity, and clutch size in purple martins. *Science* 22: 1000-1003.

Parr, C.L., P. Eggleton, A.B. Davies, T.A. Evans, and S. Holdsworth. 2016. Supression of savanna ants alters invertebrate composition and influences key ecosystem processes. *Ecology* 97: 1611-1617.

Price, P.W., R.F. Denno, M.D. Eubanks, D.L. Finke, and I. Kaplan. 2011. *Insect Ecology 3rd Ed*. New York: Cambridge University Press.

Porter, S.D. 1988. Impact of temperature on colony growth and developmental rates of the ant, *Solenopsis invicta*. *Journal of Insect Physiology* 34:1127-1133.

Potter, E.F. 1970. Anting in wild birds, its frequency and probable purpose. *The Auk* 87: 692-713.

Redford, K.H. 1984. The termitaria of *Cornitermes cumulans* (Isoptera, Termitidae) and their role in determining a potential keystone species. *Biotropica* 16: 112-119.

Revis, H.C., and D.A. Waller. 2004. Bactericidal and fungicidal activity of ant chemicals on feather parasites: an evaluation of anting behavior as a method of self-medication in songbirds. *The Auk* 121: 1262-1268.

Sánchez-Piñero, F., and J.M. Gómez. 1995. Use of ant-nest debris by darkling beetles and other arthropod species in an arid system in south Europe. *Journal of Arid Environments* 31:91-104.

Scott, G. 2010. *Essential Ornithology*. New York: Oxford University Press.

Shields, W.M., and J.R. Crook. 1987. Barn swallow coloniality: A net cost for group breeding in the Adirondacks? *Ecology* 68: 1373-1386.

Smallwood, J., and D. Culver. 1979. Colony movements of some North American ants. *Journal of Animal Ecology* 48: 373-382.

Smith, M.R. 1928. The biology of *Tapinoma sessile* Say, an important house-infesting ant. *Annals of the Entomological Society of America* 21: 307-330.

Suarez, A.V., and T.J. Case. 2005. Impacts of Argentine ants on avian nesting success. *Insectes Sociaux* 52: 378-382.

Wagner, D., M.J.F. Brown, and D.M. Gordon. 1997. Harvester ant nests, soil biota and soil chemistry. *Oecologia* 112: 232-236.

Whitford, W.G., and Y. Steinberger. 2010. Pack rats (*Neotoma* spp.): Keystone ecological engineers? *Journal of Arid Environments* 74: 1450-1455.

Willis, E.O., and Y. Oniki. 1978. Birds and army ants. *Annual Review of Ecology and Systematics* 9: 243-263.

Young, B.E., M. Kaspari, and T.E. Martin. 1990. Species-specific nest site selection by birds in ant-Acacia trees. *Biotropica* 22: 310-315.