

Prevalence and consequences of ants and other arthropods in active nests of Midwestern birds

J.C. Gibson, A.V. Suarez, D. Qazi, T.J. Benson, S.J. Chiavacci, and L. Merrill

Abstract: Many organisms build nests which create unique microhabitats that are exploited by other animals. In turn, these nest colonizers may positively or negatively influence nest owners. Bird nests are known to harbor communities that include both harmful and possibly beneficial species. We quantified the nest arthropod communities of 10 bird species in Illinois, USA, along a land-use gradient, focusing on ant prevalence. We found eight ant species in nests, and for three species, at least part of their colonies inhabited nests. The odorous house ant (*Tapinoma sessile* (Say, 1836)) was the most common species and maintained the largest colonies in nest material. Forest-cover percentage surrounding bird nests best predicted ant-colony presence. There was little evidence that ant presence influenced abundance or prevalence of other arthropods within nests with the exception of Brown Thrasher (*Toxostoma rufum* (Linnaeus, 1758)) nests, where a negative association between *T. sessile* presence and abundance of fly larvae was found. Breeding success did not differ between nests with and without ant colonies for any bird species. Ant species that exhibit polydomy and nomadism may be more likely to occupy ephemeral resources like bird nests than other ants. How widespread this phenomenon is and the degree of commensalism that both parties experience is unclear and warrants further investigation.

Key words: ants, *Tapinoma sessile*, commensalism, nest cohabitation.

Résumé : De nombreux organismes construisent des nids qui créent des microhabitats singuliers exploités par d'autres animaux. Ces colonisateurs de nid peuvent en retour avoir une influence positive ou négative sur les propriétaires des nids. Il est bien établi que les nids d'oiseaux abritent des communautés qui comprennent des espèces tant nuisibles que potentiellement bénéfiques. Nous avons quantifié les communautés d'arthropodes dans les nids de 10 espèces d'oiseaux en Illinois (États-Unis) le long d'un gradient d'utilisation du sol, en mettant l'accent sur la prévalence de fourmis. Nous avons relevé huit espèces de fourmis dans des nids, dont trois espèces dont des colonies occupaient au moins partiellement les nids. La fourmi odorante (*Tapinoma sessile* (Say, 1836)) était l'espèce la plus répandue et maintenait les plus grandes colonies dans des matériaux de nid. Le pourcentage de couvert forestier autour des nids d'oiseaux était la variable qui prédisait le mieux la présence de colonies de fourmis. Il y avait peu de preuves d'une influence de la présence de fourmis sur l'abondance ou la prévalence d'autres arthropodes dans les nids, à l'exception des nids de moqueur roux (*Toxostoma rufum* (Linnaeus, 1758)), pour lesquels une association négative entre la présence de *T. sessile* et l'abondance de larves de mouche a été notée. Aucune des espèces d'oiseaux ne présentait de différence sur le plan du succès de reproduction entre les nids avec et sans colonie. Les espèces de fourmis qui font preuve de polydomy et de nomadisme pourraient être plus susceptibles d'occuper des ressources éphémères comme des nids d'oiseaux que d'autres fourmis. L'étendue de ce phénomène et l'ampleur du commensalisme dont les deux parties font preuve ne sont pas bien établies et nécessitent plus d'études. [Traduit par la Rédaction]

Mots-clés : fourmis, *Tapinoma sessile*, commensalisme, cohabitation dans les nids.

Introduction

Community composition and structure depend on the abiotic and biotic properties of the environment. Many animals depend on “ecosystem engineers” that modify their environment, thereby creating suitable microhabitats exploited by other taxa (Jones et al. 1994). These modifications take many forms and can be chemical or physical in nature (Wright and Jones 2006). Nest construction is an example of a physical modification to the environment that can provide shelter from predation and environmental conditions

for the nest builder and other species (Redford 1984; Wagner et al. 1997; Whitford and Steinberger 2010). Nesting animals can also chemically alter the microhabitat within the nest through waste secretions (Sánchez-Piñero and Gómez 1995).

Birds are well known for their nest-building behavior and species range from creating simple scratches on the ground that barely persist for a single breeding period to complex structures that can be used for generations (Hansell 2000; Scott 2010). In addition to housing the bird eggs and nestlings, these nests can host a large diversity of arthropods (Hicks 1959; Di Iorio and

Received 29 June 2018. Accepted 18 February 2019.

J.C. Gibson. Department of Entomology, University of Illinois at Urbana–Champaign, 320 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801, USA.

A.V. Suarez. Department of Entomology, University of Illinois at Urbana–Champaign, 320 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801, USA; Department of Animal Biology, University of Illinois at Urbana–Champaign, 515 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801, USA.

D. Qazi. School of Integrative Biology, University of Illinois at Urbana–Champaign, 286 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801, USA.

T.J. Benson and L. Merrill. Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana–Champaign, Champaign, IL 61820, USA.

S.J. Chiavacci. Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana–Champaign, Champaign, IL 61820, USA; United States Geological Survey, Science and Decisions Center, 12201 Sunrise Valley Drive Reston, VA 20192, USA.

Corresponding author: Josh C. Gibson (email: jcgibso2@illinois.edu).

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from [RightsLink](https://www.rightslink.com).

Turienzo 2009). Many of these 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 Crook 1987; Møller 1990) and inducing premature fledging (Moss and Camin 1970; Møller 1990) and nest desertions (Duffy 1983). This is by no means the rule, however, and in many instances, high parasite loads in nests appear to have no direct fitness consequences to the residents (Brown and Brown 1986; Lehmann 1993). Although interactions between birds and their parasites are well studied, the ability of other nest-dwelling arthropods to influence this relationship is unclear.

Ants are ecologically successful organisms and can profoundly affect the communities in which they occur (Goheen and Palmer 2010; Parr et al. 2016). Birds have evolved fascinating mutualisms with ants, including “anting” behavior and army ant – ant bird foraging associations of the New World tropics (Potter 1970; Willis and Oniki 1978; Revis and Waller 2004; Brumfield et al. 2007). Some ants also occasionally associate with bird nests. Workers of many ant species have been found in the nests of birds (Hicks 1959; Blem and Blem 1994; Di Iorio and Turienzo 2009) and can even kill nestlings (reviewed in Suarez et al. 2005; DeFisher and Bonter 2013). A few ant species have been documented occupying bird nests, wherein ants will move all or a significant portion of their colony into the nest material (Smith 1928; Fessl et al. 2006; Lambrechts et al. 2008; Gouveia et al. 2012; Lambrechts and Schatz 2014; Mitrus et al. 2016; Maziarz et al. 2018). However, despite the huge number of studies conducted on nesting birds, documentation of ants occupying bird nests has rarely been reported, making it difficult to accurately assess how frequent this phenomenon is or the effect it could have on birds. The presence of ants could positively or negatively affect bird fitness in several ways. Ants could potentially increase breeding success by decreasing parasite load or altering the arthropod community within bird nests through predation or defensive behaviors. For example, Brown et al. (2015) found that predation of *Crematogaster lineolata* (Say, 1836) ants on swallow bugs (*Oeciocacus vicarius* Horvath, 1912) in the nests of Cliff Swallows (*Petrochelidon pyrrhonota* (Vieillot, 1817)) dramatically reduced the abundance of swallow bugs within nests. In nests of Galápagos finches (Darwin’s finches), the introduced ectoparasitic fly *Philornis downsi* Dodge and Aitken, 1968 appears to be reduced in abundance when *Camponotus* Mayr, 1861 ants colonize nests, although this observation is anecdotal (Fessl et al. 2006). Many ants produce chemicals known to be antimicrobial in nature, and in sufficient doses, these chemicals may help to kill harmful microbes within bird nests (Revis and Waller 2004). Alternatively, ants could decrease bird fitness by increasing rates of nestling mortality, premature fledging, and nest abandonment. For example, the invasive European fire ant (*Myrmica rubra* (Linnaeus, 1758)) has been shown to negatively impact Herring Gull (*Larus argentatus* Pontoppidan, 1763) reproduction by causing erratic incubation periods and predated on nestlings (DeFisher and Bonter 2013). Argentine ants (*Linepithema humile* (Mayr, 1868)) and red imported fire ants (*Solenopsis invicta* Buren, 1972) will also depredate nestlings of multiple bird species in their introduced ranges (Suarez et al. 2005). Overall, the effects of ants occupying bird nests on bird success has rarely been investigated and warrants additional study.

We investigated the associations between ant presence, nest arthropod communities, and nest success in the nests of 10 common bird species in Illinois, USA. Specifically, we were interested in addressing three main aspects of this relationship: (1) we exam-

ine which ant species colonize bird nests in Illinois and test the hypothesis that the prevalence of ants in bird nests varies by bird species; (2) we test the hypothesis that differences in landscape composition around bird nests will affect ant colonization rates; and (3) we test the competing hypotheses that the presence of ant colonies in nests will positively or negatively affect bird breeding success, either directly or by reducing the abundance of other arthropod groups in the nests which ant colonies occur.

Materials and methods

Bird species and nest monitoring

Bird nests at 10 sites in Illinois were monitored from April through July of 2014 and May through July of 2015 as part of the experiments conducted by Merrill et al. (2016) and were subsequently used in the current study (Supplementary Table S1).¹ Bird nests were located by systematically searching optimal nesting habitats at each study site and by using targeted searches in areas where adult birds exhibited nesting behaviors, including alarm-calling. Nests from 10 bird species were located using these methods (Table 1). All nest searching and monitoring work was covered by Institutional Animal Care and Use Committee (IACUC) permit No. 10127 to T.J.B. The approximate nest height and a qualitative description of the composition of each nest was recorded (Table 1). All nests were marked with flagging tape placed at least 5 m from the nest and were re-examined every 3 days for the presence of eggs, hatchlings, and fledglings. On the first nest check following fledging or nest failure (i.e., at most 3 days after fledging or nest failure occurred), nests were collected, placed in plastic Ziploc bags, and individually labeled. Nests were collected under IACUC permit No. 14072 and United States Fish and Wildlife Service (USFWS) permit No. MB31458B-0 to T.J.B. A dichotomous scoring system was used to assess breeding success due to uncertainty regarding how many chicks actually fledged from nests. Nests were scored as successful if at least one chick (including Brown-headed Cowbird (*Molothrus ater* (Boddaert, 1783)) chicks) fledged from the nest and as having failed if no chicks fledged. Nest collecting occurred from June through early August in 2014 and from 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.

Land-cover assessment

The proportion of five major land-cover types (developed, shrubland-grassland, forest, wetland, and crop) within 500 m of each nest was assessed using ArcGIS version 10.2 (ESRI 2011) and geospatial modeling environment (GME) (Beyer 2012). We selected 500 m buffers around each nest as a distance that should fully encompass the ants foraging activities, as well as any environmental influences on the nest as a direct or indirect result of land type surrounding the nest (temperature, food availability, humidity, etc.). We used the United State Department of Agriculture National Agricultural Statistics Service’s CropScape (USDA NASS 2014) to extract land-cover proportions around each nest. We overlaid our land-cover layer on orthophotos to ensure nest locations were accurate, as minor errors in the recording of a nest location on a habitat edge could place the nest in a habitat in which it was not actually located. Land-cover data are displayed as 30 m pixels of different land-cover types and have been found to be highly accurate in representing actual land cover (Luman and Tweddale 2008).

¹Supplementary tables are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2018-0182>.

Table 1. Nest descriptions for the 10 species of birds included in this study.

Bird species	Total no. of nests	Mean (\pm SD) nest height (m)	Nest location	Nest description
Eastern Towhee, <i>Pipilo erythrophthalmus</i>	7	0.8 \pm 0.4	On ground or low in shrubs	Cup woven out of fine grass and supported by twigs, bark, and dead leaves
Gray Catbird, <i>Dumetella carolinensis</i>	19	1.8 \pm 0.6	Above ground in shrubs or small trees	Cup made from twigs and mud and lined with grass
Field Sparrow, <i>Spizella pusilla</i>	19	0.3 \pm 0.2	On ground	Cup woven out of fine and coarse grasses
Northern Cardinal, <i>Cardinalis cardinalis</i>	18	1.3 \pm 0.4	Above ground in shrubs or small trees	Cup made from twigs, leaves, and fine grasses
Brown Thrasher, <i>Toxostoma rufum</i>	16	1.4 \pm 0.5	Above ground in shrubs or small trees	Cup made from twigs, leaves, and grasses
American Robin, <i>Turdus migratorius</i>	50	1.9 \pm 0.6	Above ground in trees	Cup made from mud supported by grasses and twigs and lined with grass
Cedar Waxwing, <i>Bombycilla cedrorum</i> Vieillot, 1808	1	Not measured	Above ground in trees	Cup made from fine grasses and supported with grasses and twigs
Blue Grosbeak, <i>Passerina caerulea</i>	1	Not measured	Above ground in shrubs or small trees	Cup made from twigs and dead leaves
Eastern Kingbird, <i>Tyrannus tyrannus</i> (Linnaeus, 1758)	1	Not measured	Above ground in trees	Cup made from twigs and stems and lined with fine plant material
Indigo Bunting, <i>Passerina cyanea</i>	1	Not measured	Above ground in shrubs or small trees	Cup made from grasses and stems and lined with thin grasses

Extracting arthropods from nests

To extract arthropods, each nest was thawed and placed in a 21 cm diameter sieve (W.S. Tyler Co., Cleveland, Ohio, USA) consisting of a 1 cm mesh screen stacked on top of a 0.5 cm mesh screen and separated by a height of 2 cm. Nest material was pulled apart by hand and sealed inside the top of the sieve. The sieve was then vigorously shaken for 30 s to separate any arthropods from nest material. Sieving was repeated five times per nest to maximize the number of arthropods extracted. An exception was American Robin (*Turdus migratorius* Linnaeus, 1766) nests, which were only sieved once because they were densely packed with mud and contained many more arthropods (often tens of thousands per nest, the majority of which were mites) than feasible to sort through for this study. Material extracted from the nest was transferred to a 16.5 cm \times 11.5 cm \times 4.5 cm plastic container and examined under a dissecting microscope. Specimens were then stored in 100% ethanol. Ants were identified to species using Coovert (2005), whereas other arthropods were identified to order. Bird nests were classified as possessing foraging workers 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, and as possessing an ant colony if both workers and either brood and (or) queens were found.

Statistics

All statistical analyses were performed in R version 3.3.3 (R Core Team 2017). The proportion of nests containing ants, either foraging workers or colonies, for each bird species was compared using χ^2 tests. To determine which landscape-level factors were important in predicting the presence of ant colonies in bird nests, a multiple logistic regression analysis was used to determine the generalized linear model that best predicted the prevalence of ants in nests. This analysis used the “step” function in R to systematically add and remove variables (i.e., bird species, nest height, and proportion of land cover consisting of forest, crops, grassland–shrubland, wetlands, and developed areas) from a null model consisting of just ant-colony prevalence in bird nests as the dependent variable and an intercept to calculate the corresponding improvement to the fit of the model using Akaike’s information criterion (AIC). This analysis was run three times, once with all ants combined into a single binary variable (i.e., ant colonies or

no ant colonies), and once each examining the presence or absence of the two most commonly encountered ants in our study (odorous house ant (*Tapinoma sessile* (Say, 1836)) and *Temnothorax curvispinosus* (Mayr, 1866)) separately, with the presence of the other species included in the model as a binary predictor variable. Final models for each analysis consisting of only variables found to significantly improve AIC scores were generated and the predictive values of each model were estimated with the Nagelkerke function in the “rcompanion” package in R. This function generates pseudo- R^2 values for the model using three methods: McFadden’s pseudo- R^2 , Cox and Snell pseudo- R^2 (also known as maximum-likelihood pseudo- R^2), and Nagelkerke pseudo- R^2 (also known as Craig and Uhler pseudo- R^2). These measurements are relative measures among similar models that provide an indication of how well the final model explains the observed data (Mangiafico 2015).

The total number of non-ant arthropods in nests with ants (i.e., workers only or colonies) vs. nests without ants for all bird species pooled were compared using a Welch’s two-sample t test. This same analysis was also repeated to compare the total number of arthropods in nests with ant colonies to nests without ant colonies. Mean abundance for each of the arthropod orders encountered in this study, excluding ants, was calculated by averaging the total number of individuals in a given order for each bird species. These values were compared between nests with and without *T. sessile* colonies for each bird species using a Welch’s two-sample t test for each order. The effect of other ant species on arthropod abundance was not examined because the sample size of *T. curvispinosus* colonies was too small and *Crematogaster cerasi* Fitch, 1855, the third most abundant ant in this study, was only found colonizing American Robin nests, where arthropod abundance was not quantified. Likewise, the colony sizes of *T. curvispinosus* were substantially lower than those of *T. sessile*, and thus unlikely to affect arthropod abundance significantly (see Discussion).

Differences in breeding success (i.e., a nest did or did not fledge young, regardless of whether only host nestlings, Brown-headed Cowbird nestlings, or both fledged) between nests with ants (i.e., workers only or colonies) vs. nests without ants were compared for all bird species combined and within each bird species where a sufficient sample size existed using Fisher’s exact tests. This analysis was also run within each bird species for nests with ant

Table 2. Summary of ant occurrence in bird nests of central and northern Illinois, USA.

Ant species	AMRO	BLGR	BRTH	CEDW	EAKI	EATO	FISP	GRCA	INBU	NOCA
<i>Aphaenogaster fulva</i>			W (1)							
<i>Crematogaster cerasi</i>	W (5), C (2)		W (1)	W (1)	W (1)		W (1)	W (3)		W (4)
<i>Formica pallidefulva</i>							W (1)			
<i>Lasius alienus</i>	W (3)									
<i>Tapinoma sessile</i>	W (1), C (7)		C (8)		C (1)	C (6)	W (5), C (4)	W (1), C (6)	C (1)	W (3), C (5)
<i>Temnothorax ambiguus</i>							W (1)			
<i>Temnothorax curvispinosus</i>	W (1)	W (1)	W (4), C (1)			W (2), C (3)	W (2)	W (2), C (2)		W (6), C (1), A (1)
<i>Tetramorium immigrans</i>			W (3)					W (1)		W (1)

Note: W designates that some nests of a bird species 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; A indicates that only an alate queen was found. Numbers in parentheses denote the number of nests. AMRO: American Robin (*Turdus migratorius*); BLGR: Blue Grosbeak (*Passerina caerulea*); BRTH: Brown Thrasher (*Toxostoma rufum*); CEDW: Cedar Waxwing (*Bombicilla cedrorum*); EAKI: Eastern Kingbird (*Tyrannus tyrannus*); EATO: Eastern Towhee (*Pipilo erythrophthalmus*); FISP: Field Sparrow (*Spizella pusilla*); GRCA: Gray Catbird (*Dumetella carolinensis*); INBU: Indigo Bunting (*Passerina cyanea*); NOCA: Northern Cardinal (*Cardinalis cardinalis*).

Table 3. Colony sizes for ant species found in bird nests.

Ant species	Workers		Larvae (nest with ant colonies)	Pupae (nest with ant colonies)	Queens (nest with ant colonies)
	Nest without ant colonies	Nest with ant colonies			
<i>Tapinoma sessile</i>	10.5 (1–72; n = 6)	425 (1–2174; n = 33)	180 (1–485; n = 25)	159 (1–630; n = 27)	1 (1–28; n = 21)
<i>Temnothorax curvispinosus</i>	3 (1–36; n = 16)	19 (3–29; n = 7)	3.5 (1–4; n = 4)	1 (1–17; n = 7)	1 (1–1; n = 2)
<i>Crematogaster cerasi</i> *	4 (1–202; n = 12)	NA	NA	NA	NA
<i>Tetramorium immigrans</i>	5 (1–53; n = 5)				
<i>Temnothorax ambiguus</i>	2 (n = 1)				
<i>Aphaenogaster fulva</i>	2 (n = 1)				
<i>Formica pallidefulva</i>	1 (n = 1)				
<i>Lasius alienus</i> †	NA (n = 3)				

Note: Numbers are median values with the range of values observed and sample size in parentheses. Data on ants from American Robin (*Turdus migratorius*) nests are excluded from this table, as only the presence of ant workers, queens, and brood was noted for nests of this bird species. Empty cells denote data that do not exist because no colonies of those species of ants were found in bird nests and NA is not available.

*Colonies of *C. cerasi* were only found in American Robin nests, so only worker numbers in nests without colonies are included in this table.

†*Lasius alienus* workers were only found in American Robin nests, so numerical data are not available for this species.

colonies vs. nests without ant colonies, and for nests with and without *T. sessile* colonies specifically. A multiple regression analysis to find the best-fit generalized linear model was run to determine the best model that predicted fledging success based on arthropod abundances within nests. This model included bird species, ant presence regardless of species (workers or colonies), ant-colony presence regardless of species, *T. sessile* presence (workers or colonies), *T. sessile* colony presence, *T. sessile* worker abundance, total arthropod abundance (excluding ants), abundance of fly larvae and pupae (Diptera), and mite abundance as predictive variables. The presence and abundance of other ant species were not included as separate variables in this model due to their low abundance within nests, making them unlikely to significantly influence breeding success compared with *T. sessile*. Likewise, only Diptera and mite abundance were included separately because these taxa were both the most abundant in nests and contain parasitic members that could negatively affect breeding success. Predictability of the final models were assessed using McFadden's pseudo- R^2 , Cox and Snell pseudo- R^2 , and Nagelkerke pseudo- R^2 , respectively. Results for all statistical tests were considered significant if they produced p values less than 0.05.

Results

Occurrence of ants in bird nests

Eight species of ants were found in the bird nests examined in this study (Table 2). Of these, only three (*Tapinoma sessile*, *Temnothorax curvispinosus*, and *Crematogaster cerasi*) had colonies or parts of colonies (defined here as containing worker ants and queens and (or) brood) established within bird nests. *Tapinoma sessile* had the highest prevalence, with workers present in 47 nests (35% of all nests collected), and had relatively large colony fragments living in nests (Table 3). *Temnothorax curvispinosus* was the second most prevalent ant, occurring in 25 nests (18.6% of total). The majority of the

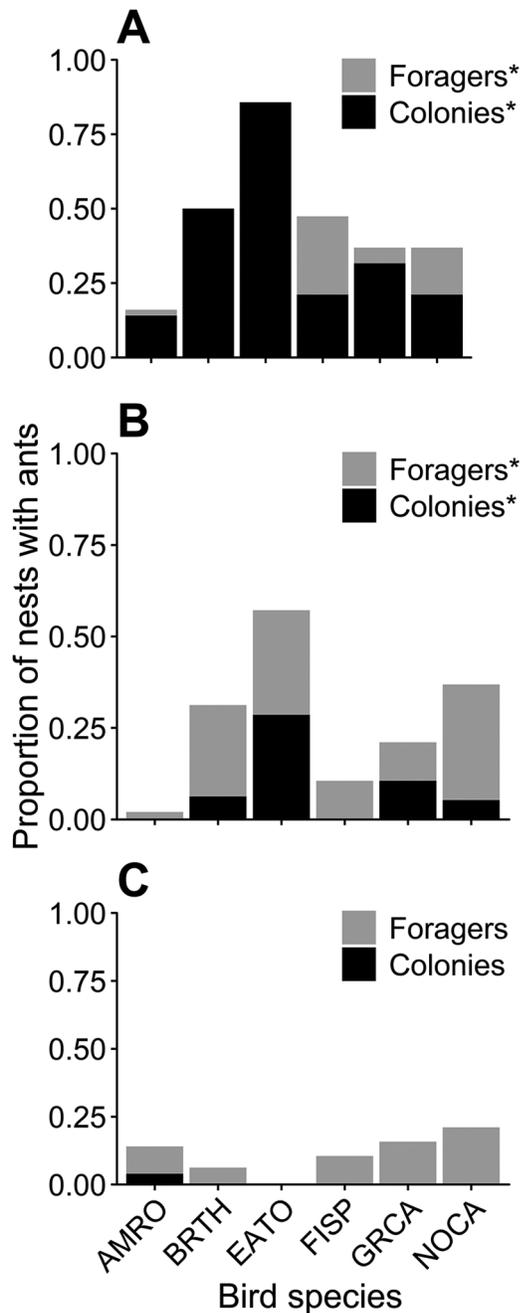
individuals encountered were workers or foragers, although occasionally small colonies of *T. curvispinosus* were found (Table 3). *Crematogaster cerasi* had foragers in 20 nests (14.9% of total) of all bird species except Blue Grosbeak (*Passerina caerulea* (Linnaeus, 1758)), Eastern Towhee (*Pipilo erythrophthalmus* (Linnaeus, 1758)), and Indigo Bunting (*Passerina cyanea* (Linnaeus, 1766)). Evidence of colonies establishing themselves in the nest only occurred in two American Robin nests. Colony size could not be accurately approximated for *C. cerasi* due to the sorting method used for American Robin nests (see Materials and methods), but both colonies had greater than 50 workers and brood. The other ant species (*Aphaenogaster fulva* Roger, 1863, *Formica pallidefulva* Latrielle, 1802, cornfield ant (*Lasius alienus* (Foerster, 1850)), *Temnothorax ambiguus* (Emery, 1895), and pavement ant (*Tetramorium immigrans* Santschi, 1927)) were only found in a small number of nests (Table 2), and only as small groups of workers (Table 3) that were likely foragers. In 22 nests the workers of two or three species of ants were found; 1 nest of Eastern Towhee contained both a colony of *T. sessile* and a colony of *T. curvispinosus*.

The prevalence of *T. sessile* colonies in nests varied among bird species (Fig. 1A; χ^2 test, $\chi^2_{[5]} = 21.7$, $p < 0.001$), as did the presence of *T. sessile* workers (Fig. 1A; χ^2 test, $\chi^2_{[5]} = 15.4$, $p = 0.009$). Similarly, the prevalence of *T. curvispinosus* colonies varied with bird species (Fig. 1B; χ^2 test, $\chi^2_{[5]} = 14.1$, $p = 0.015$), as did the prevalence of workers (Fig. 1B; χ^2 test, $\chi^2_{[5]} = 14.9$, $p = 0.011$). In contrast, the prevalence of *C. cerasi* colonies did not differ between nests of different bird species (Fig. 1C; χ^2 test, $\chi^2_{[5]} = 3.2$, $p = 0.66$), nor did the prevalence of foraging workers (Fig. 1C; χ^2 test, $\chi^2_{[5]} = 3.5$, $p = 0.62$).

Factors predicting ant prevalence

Results of the generalized linear model showed that proportion of landscape covered in forest and grassland–shrubland within 500 m were the best predictors of the presence of both all ant

Fig. 1. Prevalence of ants (odorous house ant, *Tapinoma sessile* (A); *Temnothorax curvispinosus* (B); *Crematogaster cerasi* (C)) 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 χ^2 test. Black bars represent proportion of nests containing ant colonies and gray bars represent proportion of nests containing foraging workers. The number of nests examined for each bird species are as follows — American Robin (*Turdus migratorius*; AMRO): 50; Brown Thrasher (*Toxostoma rufum*; BRTH): 16; Eastern Towhee (*Pipilo erythrophthalmus*; EATO): 7; Field Sparrow (*Spizella pusilla*; FISP): 19; Gray Catbird (*Dumetella carolinensis*; GRCA): 19; Northern Cardinal (*Cardinalis cardinalis*; NOCA): 19.



colonies regardless of species and *T. sessile* colonies in bird nests, with ant presence being positively associated with forest cover and grassland-shrubland (Table 4; Supplementary Tables 2 and 3); the fit of either model was not significantly improved by add-

Table 4. Analysis of maximum-likelihood estimates for the best-fit generalized linear model to determine habitat factors predicting the presence of ant colonies in bird nests.

Model	Parameter	df	Estimate*	SE	z	Pr > z
All ants combined	Intercept	86	1.25	0.49	2.55	0.011
	Forest	86	-2.22	1.05	-2.12	0.034
	Grassland-shrubland	86	-0.66	1.41	-0.47	0.64
<i>Tapinoma sessile</i> only	Intercept	86	2.06	0.58	3.54	0.0004
	Forest	86	-3.13	1.14	-2.76	0.0057
	Grassland-shrubland	86	-0.98	1.56	-0.63	0.53

Note: Only variables that improve the Akaike's information criterion score of the model over the null are included in the final model. Forest and grassland-shrubland represent the proportion of these land-cover types within 500 m of each nest.

*Negative values are positively associated with ant colony presence, whereas positive values are negatively associated with ant colony presence.

ing bird species, presence of *T. curvispinosus* colonies, or proportion of land covered in developed areas, crops, or wetlands (Supplementary Tables 2 and 3).¹ The final model for all ants combined explained between 28% and 47% of variance observed in colony prevalence compared with the null model, whereas the *T. sessile* model explained between 30% and 47% of variance compared with the null model (Table 5). In contrast, no input variables significantly improved the prediction of *T. curvispinosus* colonies in bird nests over the null model (Supplementary Table S4),¹ suggesting that *T. sessile* colonies drive the results of the model when the colonies of all ant species are treated as a single variable.

Effects of *Tapinoma sessile* colonies on nest arthropod communities and breeding success

Overall arthropod communities in the bird nests examined were highly variable in the number and diversity of arthropods present (Table 6). The total number of arthropods present in nest containing any ants did not differ from nests containing no ants (Welch's two-sample *t* test, $t_{[35.5]} = -0.46$, $p = 0.65$), nor did total number of arthropods differ between nests containing ant colonies and nests lacking colonies (Welch's two-sample *t* test, $t_{[58.3]} = -1.3$, $p = 0.21$). The total number of arthropods was lower in Brown Thrasher (*Toxostoma rufum* (Linnaeus, 1758)) nests containing *T. sessile* colonies (Welch's two-sample *t* test, $t_{[8.5]} = -2.7$, $p = 0.026$), but not in Northern Cardinal (*Cardinalis cardinalis* (Linnaeus, 1758)) nests (Welch's two-sample *t* test, $t_{[9.2]} = .27$, $p = 0.79$) or Gray Catbird (*Dumetella carolinensis* (Linnaeus, 1766)) nests (Welch's two-sample *t* test, $t_{[10.9]} = -0.1$, $p = 0.93$). Field Sparrow (*Spizella pusilla* (A. Wilson, 1810)) and Eastern Towhee nests were not included in these analyses due to small sample sizes for nests with and without *T. sessile* colonies. At the ordinal level, flies (Diptera) were less abundant in Brown Thrasher nests with *T. sessile* colonies compared with those without (Table 6; Welch's two-sample *t* test, $t_{[6.2]} = -3.6$, $p = 0.01$). No other insect order differed in abundance between nests with and without *T. sessile* colonies in Brown Thrasher, Northern Cardinal, or Gray Catbird nests (Table 6).

The presence of ants, ant colonies, or *T. sessile* colonies specifically did not have a detectable effect on breeding success across bird species; these results were maintained when each bird species was examined individually (Table 7). The inclusion of total arthropod abundance, abundance of fly larvae, mite abundance, *T. sessile* worker abundance, or *T. sessile* colony presence did not improve the fit of the generalized linear model for breeding success over the null model (Supplementary Table S5);¹ however, abundance of fly larvae was marginally significant, with nests containing more fly larvae being more likely to fledge chicks (Table 8; Supplementary Table S5).¹ The generalized linear model for breeding success with fly abundance as the sole predictor variable explained between 27% and 45% of variance in fledging success compared with the null model (Table 9).

Table 5. Pseudo- R^2 values for the generalized linear model predicting the presence of ant colonies in bird nests.

Model	Pseudo- R^2 type	Pseudo- R^2
All ants combined	McFadden	0.28
	Cox and Snell (maximum-likelihood)	0.39
	Nagelkerke (Cragg and Uhler)	0.47
<i>Tapinoma sessile</i> only	McFadden	0.30
	Cox and Snell (maximum-likelihood)	0.38
	Nagelkerke (Cragg and Uhler)	0.47

Discussion

Occurrence of ants in bird nests

We investigated a previously recognized but poorly understood association of birds and ants: the colonization of bird nests by ants (Smith 1928; Fessl et al. 2006; Lambrechts et al. 2008; Gouveia et al. 2012; Lambrechts and Schatz 2014; Mitrus et al. 2016; Maziarz et al. 2018). *Tapinoma sessile* was by far the most prevalent ant species encountered in this study and had the largest colonies (e.g., as many as 2000 workers and 30 queens in a single nest). Many aspects of the biology of *T. sessile* may explain its ability to exploit bird nests as a resource, including a high degree of polydomy and polygyny and a propensity to relocate nesting locations multiple times during a single season (Smith 1928; Buczkowski and Bennett 2008).

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 (Covert 2005). The appearance of *T. curvispinosus* colonies in bird nests is surprising considering its reputation as a litter-dwelling species. However, *T. curvispinosus* workers are known to forage semi-arborescally, sometimes appearing at the extrafloral nectaries of bigtooth aspen (*Populus grandidentata* Michx.) (Davis and Bequaert 1922). All of the bird species with which *T. curvispinosus* were found to associate incorporate many sticks and twigs into their nests. It is therefore possible that these colonies were accidentally moved into nests of birds through the transport of nest construction material, which would explain the discrepancy between the ordinary nesting habits of this species and their occurrence in bird nests in this study.

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 (Covert 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 with the other two commonly encountered species in this study.

The nesting habits of these ants may help inform what characteristics allow them to use 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 that they modify very little (Smith 1928; Covert 2005). Both *T. sessile* and *T. curvispinosus* are nomadic and polydomous, allowing them to exploit temporary nesting resources (Smith 1928; Hölldobler and Wilson 1990; Covert 2005). 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 traits likely make these species more likely to use bird nests as a nesting resource.

Table 6. Occurrence data for arthropod orders in Brown Thrasher (*Toxostoma rufum*), Gray Catbird (*Dumetella carolinensis*), and Northern Cardinal (*Cardinalis cardinalis*) nests with and without *Tapinoma sessile* colonies.

Arthropod order	No. of nests		Mean (\pm SD) abundance	
	Without ants	With ants	Without ants	With ants
Brown Thrasher				
Acari: mites	6	5	57.2 \pm 111.9	18.0 \pm 16.4
Acari: ticks	0	1	NA	1.0
Araneae	1	4	2.0	1.8 \pm 1.5
Blattodea	0	1	NA	12.0
Chilopoda	0	1	NA	4.0
Coleoptera	4	0	5.3 \pm 1.0	NA
Collembola	5	5	11.6 \pm 10.6	4.8 \pm 3.8
Dermaptera	3	2	7.7 \pm 9.9	14.0 \pm 8.5
Diplopoda	2	1	8.0 \pm 9.9	1.0
Diptera*	7	10	103 \pm 64.0	14.6 \pm 10.5
Hemiptera	1	3	5.0	2.0 \pm 1.7
Hymenoptera	4	1	1.0 \pm 0.0	3.0
Isopoda	2	4	7.0 \pm 5.7	3.0 \pm 2.5
Lepidoptera	2	1	2.0 \pm 1.4	1.0
Opiliones	1	1	1.0	1.0
Pseudoscorpiones	1	0	1.0	NA
Psocoptera	1	3	1.0	1.3 \pm 0.6
Thysanoptera	3	1	1.7 \pm 0.6	34.0
Miscellaneous	4	2	2.5 \pm 1.7	11.0 \pm 12.7
Gray Catbird				
Acari: mites	10	6	253.1 \pm 744.3	166.5 \pm 350.9
Araneae	4	3	1.8 \pm 1.0	1.7 \pm 1.2
Chilopoda	1	1	1.0	1.0
Coleoptera	6	6	1.8 \pm 0.8	2.7 \pm 2.4
Collembola	8	4	19.3 \pm 42.5	4.8 \pm 5.0
Dermaptera	2	3	1.0 \pm 0.0	16.3 \pm 24.0
Diptera	12	7	28.2 \pm 31.0	44.3 \pm 63.8
Hemiptera	6	4	25.8 \pm 44.2	2.3 \pm 2.5
Hymenoptera	2	2	2.0 \pm 0.0	1.0 \pm 0.0
Isopoda	2	3	34.5 \pm 46.0	9.3 \pm 5.9
Lepidoptera	6	3	8.0 \pm 7.9	2.7 \pm 2.9
Orthoptera	0	1	NA	1.0
Psocoptera	2	1	3.5 \pm 0.7	1.0
Siphonaptera	3	0	2.3 \pm 2.3	NA
Thysanoptera	4	2	7.5 \pm 11.0	1.5 \pm 0.7
Miscellaneous	1	3	NA	1.7 \pm 1.2
Northern Cardinal				
Acari: mites	10	4	276.8 \pm 865.8	8.0 \pm 11.0
Araneae	0	1	NA	2.0
Chilopoda	1	0	1.0	NA
Coleoptera	8	3	1.8 \pm 0.9	7.3 \pm 10.1
Collembola	8	1	10.6 \pm 24.4	5.0
Diplopoda	3	0	2.0 \pm 1.0	NA
Diptera	16	5	9.6 \pm 12.8	32.2 \pm 55.0
Hemiptera	4	1	3.0 \pm 2.8	22.0
Hymenoptera	1	2	3.0	1.5 \pm 0.7
Isopoda	2	1	9.5 \pm 6.4	2.0
Lepidoptera	3	0	2.3 \pm 1.5	NA
Neuroptera	1	0	1.0	NA
Opiliones	2	0	1.0 \pm 0.0	NA
Psocoptera	0	1	NA	2.0
Thysanoptera	3	2	1.7 \pm 0.6	21.0 \pm 26.9
Miscellaneous	4	2	1.5 \pm 1.0	1.0 \pm 0.0

Note: No. of nests refers to the number of nests of a bird species containing members of an arthropod order. Hymenoptera numbers exclude any ants. The miscellaneous category includes any arthropod parts that were unidentifiable to order. NA is not available.

*Mean (\pm SD) abundance significantly differs between nests with ants and nests without ants according to a Welch's two-sample *t* test ($p < 0.05$).

Table 7. Results of Fisher's exact tests comparing fledging success between bird (American Robin (*Turdus migratorius*), Brown Thrasher (*Toxostoma rufum*), Eastern Towhee (*Pipilo erythrophthalmus*), Field Sparrow (*Spizella pusilla*), Gray Catbird (*Dumetella carolinensis*), Northern Cardinal (*Cardinalis cardinalis*)) nests with and without ants.

Nest data set	Nests with ants		Nests without ants		Fisher's exact test	
	No. of fledging nests	No. of failed nests	No. of fledging nests	No. of failed nests	Odds ratio	<i>p</i>
All nests	30	40	29	21	1.83	0.14
American Robin	8	5	21	7	1.84	0.47
Brown Thrasher	5	7	2	2	1.37	1.00
Eastern Towhee	2	6	0	1	0.00	1.00
Field Sparrow	3	8	3	4	1.92	0.63
Gray Catbird	7	6	2	2	0.86	1.00
Northern Cardinal	5	6	1	5	0.26	0.33

Nest data set	Nests with ant colony		Nests without ant colony		Fisher's exact test	
	No. of fledging nests	No. of failed nests	No. of fledging nests	No. of failed nests	Odds ratio	<i>p</i>
All nests	19	23	40	38	1.27	0.57
American Robin	6	3	23	9	1.27	1.00
Brown Thrasher	3	6	4	3	2.50	0.61
Eastern Towhee	2	6	0	1	0.00	1.00
Field Sparrow	1	2	5	10	1.00	1.00
Gray Catbird	5	3	4	5	0.50	0.64
Northern Cardinal	2	2	4	9	0.47	0.58

Nest data set	Nests with <i>Tapinoma sessile</i> colony		Nests without <i>T. sessile</i> colony		Fisher's exact test	
	No. of fledging nests	No. of failed nests	No. of fledging nests	No. of failed nests	Odds ratio	<i>p</i>
All nests	15	19	44	41	1.36	0.54
American Robin	4	3	25	9	2.04	0.40
Brown Thrasher	3	5	4	4	1.61	1.00
Eastern Towhee	2	4	0	1	0.00	1.00
Field Sparrow	1	2	5	10	1.00	1.00
Gray Catbird	3	3	6	5	1.19	1.00
Northern Cardinal	2	1	4	10	0.22	0.51

Table 8. Analysis of maximum-likelihood estimates for the best-fit generalized linear model to determine the influence of arthropod abundance on fledging success.

Parameter	df	Estimate*	SE	<i>z</i>	Pr > <i>z</i>
Intercept	89	-0.52	0.25	-2.12	0.034
Diptera abundance	89	0.015	0.0078	1.96	0.051

Note: Only arthropod taxa that improve the Akaike's information criterion score of the model over the null are included in the final model.

*Positive values are positively associated with fledging success, whereas negative values are negatively associated with fledging success.

These traits are not restricted to the ants encountered in this study and are common in many ant species (Hölldobler and Wilson 1990; Lach et al. 2010), suggesting that the colonization of bird nests might be a widespread behavior in ants. Inhabiting bird nests likely provides a number of benefits to ant colonies, such as protection provided by the physical structure of nests or the elevated temperatures provided by the presence of eggs and brooding parents, which can speed up developmental times of ant larvae (Porter 1988; Hartley and Lester 2003). Access to nutritional resources within the nests, including nestling excrement, feather dander, and other nest-dwelling arthropods, is also a possible benefit.

Effects of landscape on ant prevalence in bird nests

The prevalence of *T. sessile* within nests among sites increased with increasing forest cover. *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). This relationship could thus potentially be explained by an increasing abundance of *T. sessile* colonies with increasing forest

Table 9. Pseudo- R^2 values for the generalized linear model predicting fledging success based on arthropod abundance.

Pseudo- R^2 type	Pseudo- R^2
McFadden	0.27
Cox and Snell (maximum-likelihood)	0.38
Nagelkerke (Cragg and Uhler)	0.45

cover, although we do not have data on abundance of *T. sessile* outside of bird nests at each site to support this. We did not collect data relevant to the stage of nest construction when ants move into bird nests, or for how long they remain after the nests have been abandoned. However, 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 (Smallwood and Culver 1979; Meissner and Silverman 2001) warrants future investigation of this aspect of the relationship.

Effects of ants on arthropod communities and breeding success

The arthropod communities in the bird nests examined in this study were highly variable in terms of the taxa and number of arthropods, but they were consistent with groups known to occur in bird nests (Hicks 1959). Many of these groups are likely facultatively associating with bird nests, 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 obligately associating with bird nests as ectoparasites. Many ecto-

parasitic 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. In examining the association between ants and other nest arthropods, the only effect we found was a negative effect of *T. sessile* on the abundance of fly larvae and pupae in the nests of Brown Thrashers. This suggests that while *T. sessile* colonies may 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 (family Calliphoridae) that are known to significantly affect the health of nestlings in some species of birds via exsanguination (Lehmann 1993). Why the effect of *T. sessile* on fly abundance is restricted to Brown Thrasher nests is unknown, but it could be due to 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 the abundance of flies or other arthropods in bird nests may be widespread, as suggested by similar findings in previous studies (Fessl et al. 2006; Brown et al. 2015).

In Brown Thrasher nests, the reduction of fly abundance associated with the presence of *T. sessile* colonies did not appear to affect breeding success because there was no statistical difference in the number of successful nests between Brown Thrasher nests with or without *T. sessile* colonies. Likewise, no other species of bird was found to have differential breeding success rates in nests with *T. sessile* colonies compared with those without, and the results of the generalized linear model suggest that the abundance of key arthropod taxa do not have any effect on breeding success. Thus *T. sessile* likely is a tolerated facultative commensalist in bird nests, although any effects *T. sessile* could have on breeding 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. In addition, there may be subtle effects on nestling or fledgling condition that did not manifest as differences in breeding success, but which could have long-term effects on the health and fitness of the birds.

Conclusions

The 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 documented 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. Focused studies on a single ant – bird nest interaction, such as *T. sessile* and Brown Thrashers, will also increase our understanding of the positive, negative, or neutral effects each species involved may receive.

Acknowledgements

We thank members of the field crew (K. Ripple, E. Ospina, M. Olsta, J. Newton, C. Elkins, E. Peterson, V. Lima, O. Paris, A. Ondrejch, L. Novak, P. Dickson, S. Darcy, and M. Helfrich), as well as R. Kayser, S. Yadron, K. Rola, J. Lao, and B. Rao, for help sorting arthropods in the laboratory. S. Ruzi, R. Achury, K. Drager, M. Rivera, B. Allan, and M. Ward provided support and constructive comments on the manuscript. Thanks also go to S. Buck for access to the University of Illinois' Vermilion River Observatory, the Champaign County Forest Preserve District, the Urbana Parks District and D. Liebert, the Forest Preserve District of Kane County, and the Illinois Department of Natural Resources (IDNR) for use of their properties. Funding was provided by the USFWS and IDNR Federal Aid in Wildlife Restoration grant number W-181-R to T.J.B. and the Illi-

nois Natural History Survey as part of a postdoctoral fellowship to L.M. We declare no conflicts of interest.

References

- Belcher, A.K., Berenbaum, M.R., and Suarez, A.V. 2016. Urbana house ants 2.0: Revisiting M. R. Smith's 1926 survey of house-infesting ants in central Illinois after 87 years. *Am. Entomol.* **62**: 182–193. doi:10.1093/ae/tmw041.
- Beyer, H.L. 2012. Geospatial modeling environment. Version 0.7.2.1 software. Available from <http://www.spatial ecology.com/gme> [accessed 1 February 2016].
- Blem, C.R., and Blem, L.B. 1994. Composition and microclimate of Prothonotary Warbler nests. *Auk*, **111**: 197–200. doi:10.2307/4088523.
- Brown, C.R., and Brown, M.B. 1986. Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). *Ecology*, **67**: 1206–1218. doi:10.2307/1938676.
- Brown, C.R., Page, C.E., Robison, G.A., O'Brien, V.A., and Booth, W. 2015. Predation by ants controls swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*) infestations. *J. Vector Ecol.* **40**: 152–157. doi:10.1111/jvec.12144. PMID:26047195.
- Brumfield, R.T., Tello, J.G., Cheviron, Z.A., Carling, M.D., Crochet, N., and Rosenberg, K.V. 2007. Phylogenetic conservatism and antiquity of a tropical specialization: Army-ant-following in the typical antbirds (Thamnophilidae). *Mol. Phylogenet. Evol.* **45**: 1–13. doi:10.1016/j.ympev.2007.07.019. PMID:17768072.
- Buczkowski, G., and Bennett, G. 2008. Seasonal polydomy in a polygynous supercolony of the odorous house ant, *Tapinoma sessile*. *Ecol. Entomol.* **33**: 780–788. doi:10.1111/j.1365-2311.2008.01034.x.
- Coovert, G.A. 2005. The ants of Ohio (Hymenoptera: Formicidae). *Bull. Ohio Biol. Surv.* **15**(2): 1–196.
- Davis, W.T., and Bequaert, J. 1922. An annotated list of the ants of Staten Island and Long Island N.Y. *Bull. Brooklyn Entomol. Soc.* **17**: 1–25.
- DeFisher, L.E., and Bonter, D.N. 2013. Effects of invasive European fire ants (*Myrmica rubra*) on herring gull (*Larus argentatus*) reproduction. *PLoS ONE*, **8**: e64185. doi:10.1371/journal.pone.0064185. PMID:23691168.
- Di Iorio, O., and Turienzo, P. 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. doi:10.2307/1937334.
- ESRI. 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute (ESRI), Inc., Redlands, Calif.
- Fessl, B., Kleindorfer, S., and Tebbich, S. 2006. An experimental study on the effects of an introduced parasite in Darwin's finches. *Biol. Conserv.* **127**: 55–61. doi:10.1016/j.biocon.2005.07.013.
- Goheen, J.R., and Palmer, T.M. 2010. Defensive plant–ants stabilize megaherbivore-driven landscape change in an African savanna. *Curr. Biol.* **20**: 1768–1772. doi:10.1016/j.cub.2010.08.015. PMID:20817530.
- Gouveia, F.B.P., Barbosa, M.L.L., and Barrett, T.V. 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. *J. Nat. Hist.* **46**: 979–1003. doi:10.1080/00222933.2011.651642.
- Hansell, M. 2000. Bird nests and construction behavior. Cambridge University Press, New York.
- Hartley, S., and Lester, P.J. 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. *N.Z. Entomol.* **26**: 91–100. doi:10.1080/00779962.2003.9722113.
- Hicks, E.A. 1959. Check-list and bibliography on the occurrence of insects in birds' nests. Iowa State College Press, Ames. doi:10.5962/bhl.title.6819.
- Hölldobler, B., and Wilson, E.O. 1990. The ants. Belknap Press, Cambridge, Mass.
- Jones, C.G., Lawton, J.H., and Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos*, **69**: 373–386. doi:10.2307/3545850.
- Lach, L., Parr, C.L., and Abbott, K.L. 2010. Ant ecology. Oxford University Press, New York.
- Lambrechts, M.M., and Schatz, B. 2014. Ants and Paridae share nesting boxes in continental Mediterranean habitat. *Folia Zool.* **63**: 63–66. doi:10.25225/fozo.v63.i2.a2.2014.
- Lambrechts, M.M., Schatz, B., and Bourgault, P. 2008. Interactions between ants and breeding Paridae in two distinct Corsican oak habitats. *Folia Zool.* **57**: 264–268.
- Lehmann, T. 1993. Ectoparasites: Direct impact on host fitness. *Parasitol. Today*, **9**: 8–13. doi:10.1016/0169-4758(93)90153-7. PMID:15463655.
- Luman, D., and Tweddle, T. 2008. Assessment and potential of the 2007 USDA-NASS Cropland Data Layer for statewide annual land cover applications. University of Illinois, Institute of Natural Resource Sustainability, Champaign.
- Mangiafico, S.S. 2015. An R companion for the handbook of biological statistics. Version 1.3.3. Available from <http://rcompanion.org/rcompanion/>.
- Maziarz, M., Broughton, R.K., Hebda, G., and Wesolowski, T. 2018. Occupation of wood warbler *Phylloscopus sibilatrix* nests by *Myrmica* and *Lasius* ants. *Insectes Soc.* **65**: 351–355. doi:10.1007/s00040-018-0613-z.
- Meissner, H.E., and Silverman, J. 2001. Effects of aromatic cedar mulch on the Argentine ant and the odorous house ant (Hymenoptera: Formicidae). *J. Econ. Entomol.* **94**: 1526–1531. doi:10.1603/0022-0493-94.6.1526. PMID:11777059.

- Merrill, L., Baehl, E.M., Ripple, K.E., and Benson, T.J. 2016. Do birds alter their levels of parental investment based on nest-site habitat features? *Ethology*, **122**: 859–868. doi:10.1111/eth.12535.
- Mitrus, S., Hebda, G., and Wesolowski, T. 2016. Cohabitation of tree holes by ants and breeding birds in a temperate deciduous forest. *Scand. J. For. Res.* **31**: 135–139. doi:10.1080/02827581.2015.1072239.
- Møller, A.P. 1990. Effects of parasitism by a haematophagous mite on reproduction in the Barn Swallow. *Ecology*, **71**: 2345–2357. doi:10.2307/1938645.
- Moss, W.W., and Camin, J.H. 1970. Nest parasitism, productivity, and clutch size in purple martins. *Science*, **22**: 1000–1003. doi:10.1126/science.168.3934.1000. PMID:5441019.
- Parr, C.L., Eggleton, P., Davies, A.B., Evans, T.A., and Holdsworth, S. 2016. Suppression of savanna ants alters invertebrate composition and influences key ecosystem processes. *Ecology*, **97**: 1611–1617. doi:10.1890/15-1713.1. PMID:27459790.
- Porter, S.D. 1988. Impact of temperature on colony growth and developmental rates of the ant, *Solenopsis invicta*. *J. Insect Physiol.* **34**: 1127–1133. doi:10.1016/0022-1910(88)90215-6.
- Potter, E.F. 1970. Anting in wild birds, its frequency and probable purpose. *Auk*, **87**: 692–713. doi:10.2307/4083703.
- R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.r-project.org/>.
- Redford, K.H. 1984. The termitaria of *Cornitermes cumulans* (Isoptera, Termitidae) and their role in determining a potential keystone species. *Biotropica*, **16**: 112–119. doi:10.2307/2387842.
- Revis, H.C., and Waller, D.A. 2004. Bactericidal and fungicidal activity of ant chemicals on feather parasites: an evaluation of anting behavior as a method of self-medication in songbirds. *Auk*, **121**: 1262–1268. doi:10.1642/0004-8038(2004)121[1262:BAFAOA]2.0.CO;2.
- Sánchez-Piñero, F., and Gómez, J.M. 1995. Use of ant-nest debris by darkling beetles and other arthropod species in an arid system in south Europe. *J. Arid Environ.* **31**: 91–104. doi:10.1006/jare.1995.0052.
- Scott, G. 2010. *Essential ornithology*. Oxford University Press, New York.
- Shields, W.M., and Crook, J.R. 1987. Barn Swallow coloniality: a net cost for group breeding in the Adirondacks? *Ecology*, **68**: 1373–1386. doi:10.2307/1939221.
- Smallwood, J., and Culver, D. 1979. Colony movements of some North American ants. *J. Anim. Ecol.* **48**: 373–382. doi:10.2307/4167.
- Smith, M.R. 1928. The biology of *Tapinoma sessile* Say, an important house-infesting ant. *Ann. Entomol. Soc. Am.* **21**: 307–330. doi:10.1093/aesa/21.2.307.
- Suarez, A.V., Yeh, P., and Case, T.J. 2005. Impacts of Argentine ants on avian nesting success. *Insectes Soc.* **52**: 378–382. doi:10.1007/s00040-005-0824-y.
- USDA NASS. 2014. CropScape — Cropland Data Layer. United States Department of Agriculture National Agricultural Statistics Service (USDA NASS), Washington, D.C. Available from <http://nassgeodata.gmu.edu/CropScape/> [accessed 1 February 2016].
- Wagner, D., Brown, M.J.F., and Gordon, D.M. 1997. Harvester ant nests, soil biota and soil chemistry. *Oecologia*, **112**: 232–236. doi:10.1007/s004420050305. PMID:28307575.
- Whitford, W.G., and Steinberger, Y. 2010. Pack rats (*Neotoma* spp.): Keystone ecological engineers? *J. Arid Environ.* **74**: 1450–1455. doi:10.1016/j.jaridenv.2010.05.025.
- Willis, E.O., and Oniki, Y. 1978. Birds and army ants. *Annu. Rev. Ecol. Syst.* **9**: 243–263. doi:10.1146/annurev.es.09.110178.001331.
- Wright, J.P., and Jones, C.G. 2006. The concept of organisms as ecosystem engineers ten years on: Progress, limitations and challenges. *BioScience*, **56**: 203–209. doi:10.1641/0006-3568(2006)056[0203:TCCOAE]2.0.CO;2.