Dominance of Pavement Ants (Hymenoptera: Formicidae) in Residential Areas of West Lafayette, IN, USA[1]

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Abstract Ant abundance and diversity are affected by numerous factors, including competition. Pavement ants (*Tetramorium immigrans* Santschi) are by far the most dominant species in North American urban areas, and so likely engage in interspecific competition and thus affect the abundance and diversity of other ant species. Ant abundance and diversity were monitored at the level of genus at two field sites in West Lafayette, IN, taking into account temperature, humidity, and habitat as possible factors in ant distribution. Temperature was found to be a significant factor affecting the abundance of ants, while humidity was not. The different habitats at the two locations resulted in the presence of different genera. The number of pavement ants was positively correlated with the number of cornfield ants (*Lasius neoniger* Emery) in Copper Beech Apartments, but not at Purdue Village. There was also a slightly greater diversity of ants found at Copper Beech Apartments.

Key Words ants, territory, dominance, competition

The pavement ant, whose name was recently revived from synonymy by Wagner et al. (2017), *Tetramorium immigrans* Santschi, is the most ubiquitous ant species in Indiana, and is considered a pest in and around residential buildings. Pavement ants are a dominant species in urban areas, but the consequence of this for ant diversity has not been fully explored. Arnan et al. (2011) found a negative relationship between dominant and subdominant ants as well as between subdominant and subordinate ants, but a positive relationship between dominant and subordinate ants, suggesting that dominant species promote species richness by reducing the impact of subdominant on subordinate species.

Ant abundance is affected by many factors other than competition, including temperature (Sanada-Morimura et al. 2006), humidity (Gordon and Heller 2014), and habitat (Showler et al. 1989); hence, those three factors need to be taken into account as well in this study. How the abundance of ants changes throughout the field season with weather changes also needs to be determined in order to determine the extent and possible effects of pavement ant dominance.

Two study locations were selected in West Lafayette, IN: Copper Beech Apartments (Site 1) and Purdue Village (Site 2). To study the different territories of ants around buildings, the building perimeter was divided into arbitrary “territorial

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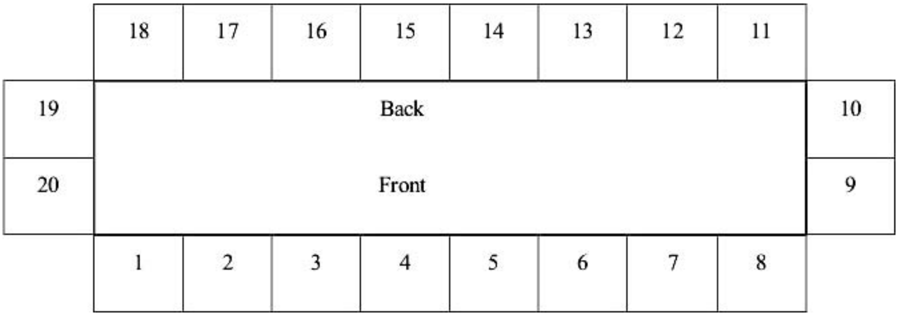

Fig. 1. Framework of "territorial units" for the Purdue Village and Copper Beech Apartment buildings.

units," and these provide a framework for placing bait stations and performing baiting surveys to determine ant abundance and diversity. These surveys allowed analysis of the interactions between pavement ant territories and subordinate ant species.

Materials and Methods

Temperature, humidity, and weather readings were taken from www.wunderground.com at Purdue University Airport in West Lafayette. Both Copper Beech Apartments (Site 1; N 40°27′16″, W 86°57′37″) and Purdue Village (Site 2; N 40°25′22″, W 86°55′44″) were residential areas. Site 1 had more variable elevation, shrubbery, shade from the sun, and many residents had dogs that they walk around the perimeter. Site 2 was flat, had large trees, had less shade, and the residents did not keep pets, and so it is squirrels that are found foraging around the buildings there.

Three apartment buildings from Site 1 (building numbers of apartments: 2761 [N 40°27′14″, W 86°57′28″] and 2788 [N 40°27′15″, W 86°57′28″] on Peachleaf Drive and 2761 [N 40°27′12″, W 86°57′28″] on Greyleaf Drive) and three apartment buildings from Site 2 (building numbers: 131 [N 40°25′18″, W 86°55′34″], 132 [N 40°25′18″, W 86°55′35″], and 1381 [N 40°25′26″, W 86°55′42″]) were used in this study. The perimeter of each building was divided into 20 territorial units as shown in Fig. 1 (eight units on each long side and two units on each short side). The 20 territorial units of each building were baited using blended tuna and corn syrup (an amount about the size of a U.S. 5-cent coin) on 2.5-inch $\times$ 3-inch note cards placed along the exterior wall in the middle of that unit. The baiting was performed in the afternoon between 1200 and 1600 h, with the ant species and abundance noted in the evening between 1700 and 2100 h and again the following morning between 0700 and 1100 h. Bait was replenished to the original amount, and missing cards were replaced at Observation 1, and then disposed of after Observation 2. The observation with the higher number of ants was used for all analyses. Surveys were conducted in 2016 every 1–2 weeks weather permitting, starting in April and ending in October.

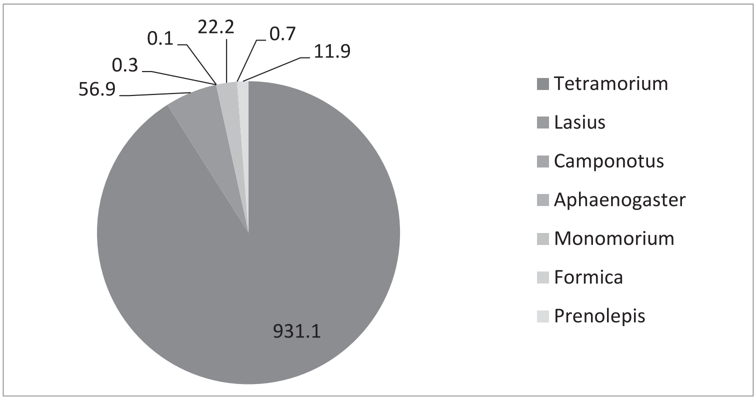

Fig. 2. Average number of ants according to genera from 24 April 2016 to 21 October 2016 around three buildings at Site 2.

Results

All ants were identified to genus, but in most cases each genus was represented by a single species. All *Tetramorium* Mayr ants found were *Tetramorium immigrans* (pavement ants), all *Lasius* F. ants found were *Lasius neoniger* Emery (cornfield ants), all *Tapinoma* Foerster ants found were *Tapinoma sessile* Say (odorous house ants), all *Solenopsis* Westwood ants found were *Solenopsis molesta* Say (thief ants), all *Monomorium* Mayr ants found were *Monomorium minimum* Buckley (little black ants), and all *Prenolepis* Mayr ants found were *Prenolepis impairs* Say. Almost all of the *Camponotus* Mayr ants found were *Camponotus pennsylvannicus* De Geer (eastern black carpenter ants), but a few individuals of other *Camponotus* species were also found; all *Camponotus* species were analyzed together. Ants from the genera *Aphaenogaster* Mayr, *Formica* L., and *Crematogaster* Lund (acrobat ants) were not identified to species and were also analyzed as a pooled genus sample. The genera of ants found at Site 2 were *Tetramorium*, *Lasius*, *Camponotus*, *Formica*, *Aphaenogaster*, *Monomorium*, and *Prenolepis*, whereas at Site 1 the genera found were *Tetramorium*, *Solenopsis*, *Crematogaster*, *Lasius*, *Tapinoma*, and *Aphaenogaster*.

In the summerlong survey of three buildings at Site 2, 91% of the ants found were pavement ants, 5.6% were cornfield ants, 2.2% were *Monomorium*, 1.2% were *Prenolepis*, 0.1% were *Formica*, 0.03% were *Camponotus*, and 0.01% were *Aphaenogaster* (Fig. 2); whereas at Site 1, 69% were pavement ants, 13% were odorous house ants, 5.4% were thief ants, 4.6% were acrobat ants, 4.5% were cornfield ants, and 3.8% were *Aphaenogaster* (Fig. 3).

The total number of ants present across these buildings was found to positively correlate significantly with mean temperature (ANOVA[Total number of ants~Mean temperature]: $F = 10.1$, df = 1, $P < 0.01$) but not humidity (ANOVA[Total number of ants~Humidity]: $F = 3.103$, df = 1, $P = 0.0972$) and a significant positive correlation was also found between the number of thief ants and mean temperature (ANOVA[Total number of thief ants~Mean temperature]: $F = 3.103$, df = 1, $P <$

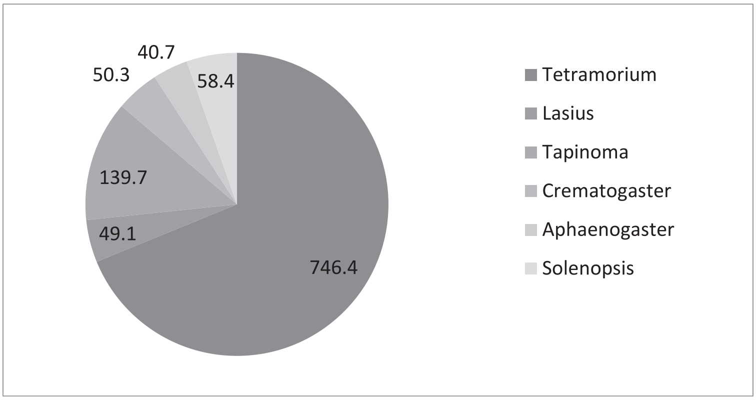

Fig. 3. Average number of ants according to genera from 24 April 2016 to 21 October 2016 around three buildings at Site 1.

0.01). However, no significant correlation was found with mean temperature for *Prenolepis* (ANOVA[Total number of *Prenolepis* ants~Mean temperature]: $F = 1.951$, df = 1, $P = 0.182$) or with humidity for *Formica* (ANOVA[Total number of *Formica* ants~Humidity]: $F = 1$, df = 1, $P = 0.332$). There was a significant positive correlation between pavement ants and cornfield ants at Site 1 (ANOVA[Total number of pavement ants~Total number of cornfield ants]: $F = 7.652$, df = 1, $P = 0.0138$; Fig. 4).

Discussion

In comparing the number of genera found at the two sites, it appears that a similar number was found, with Site 2 having slightly more diversity. Pavement ants, cornfield ants, thief ants, *Aphaenogaster*, and acrobat ants were found at both locations, while *Prenolepis*, *Camponotus*, *Formica*, and *Monomorium* were found only at Site 2 and odorous house ants were found exclusively at Site 1. The presence of *Camponotus* at Site 2 was to be expected as a number of aging trees can be found in the vicinity, but none were found at Site 1. Acrobat ants were found in abundance at Site 1, but none were found at Site 2 in 2015 and 2016, but Building 215 where they were found in 2014 was not studied in those years.

The effect of temperature is positively correlated with the total number of ants as well as very significantly correlated with the total number of thief ants. There was no significant negative correlation between temperature and the numbers of *Prenolepis*, which would be expected in a cold-adapted species (Fellers 1989). This also suggests that other factors could be involved. Humidity seems to not be significantly correlated with the number of ants, but a nonsignificant trend was seen where *Formica* was seen in higher numbers when humidity was low.

From Figs. 1 and 2, it is very clear that there is a much greater dominance of pavement ants over other ants at Site 2 compared with Site 1. The dominance of pavement ants is demonstrated clearly by their being the most abundant ant around the residential buildings at both sites. There was a significantly larger number of

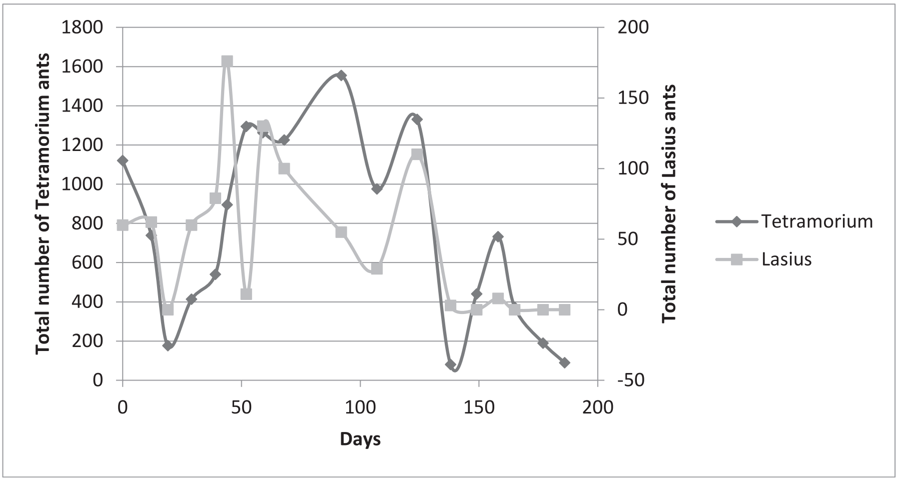

Fig. 4. Total number of pavement ants and cornfield ants around three buildings at Site 1 from 24 April 2016 to 21 October 2016.

non–pavement ants but slightly smaller total number of genera at Site 1. This may affirm the finding of Arnan et al. (2011) that larger numbers of a dominant species increases the overall diversity. This is proposed to be achieved by the dominant species controlling the abundance of subdominant species. The reduced numbers in subdominant species are then less able to control the numbers of the subordinate species. This results in an increase in the numbers of the subordinate species because their direct competitor's numbers are reduced. Cornfield ants are a possible candidate subordinate species at Site 1, as there was a positive correlation at this site between them and pavement ants. The protection of subordinate species by dominant ants can be explained by the positive relationship between dominant ants and species richness found in Australia (Andersen 1995). Odorous house ants are the second most numerous ant at Site 1, and, thus, likely function as subdominant ants. These subdominant ants likely compete directly with both the dominant pavement ants and the subordinate cornfield ants. There was no correlation between pavement ants and cornfield ants at Site 2, though, and this might be because they compete directly with pavement ants. Thus, they probably function as a subdominant ant rather than a subordinate ant. Although abundances alone cannot be used in isolation to infer competition, this can serve as a starting point for further studies, given the limitations in this study. Furthermore, there has not been evidence prior to this of a contextual dominance relationship as proposed here between functional groups of ants.

Another possible factor that may affect this dominance hierarchy might be that the different habitats of the two sites facilitate niche differentiation. Savolainen and Vepsalainen (2010) investigated *Formica polyctena* Foerster to determine how this dominant species affected habitat use by other ant species. They found that in addition to behavioral responses to the top dominant, niche differentiation also facilitates the coexistence between submissives and top dominants. The submissive species also have small colonies and short foraging distances, which also aid in allowing coexistence. Possibly the more open terrain and greater density of pavement ants at Site 2 discourages such coexistence, compared to the more varied habitat and lower-density patchiness of pavement ants at Site 1. Tanaka et al. (2012), on the other hand, examined the effect of the fern-dwelling *Crematogaster difformis* Frederick Smith on ant assemblages on emergent trees, and found that this single species can affect the structure of the entire assemblage of ants in the canopy of rainforests. They came to this conclusion because all other ant species were excluded from *Crematogaster difformis* territories, whereas conspecific trees without *Crematogaster difformis* had very different ant species assemblages. This could allow for the possibility that habitat may even be irrelevant, and that the greater numbers of pavement ants at Site 2 that determine the ant species assemblages.

Further studies involving the nest locations of these three species would be useful to determine if the dominance hierarchy at the bait stations is related to the spatial distribution of these nests. Spatial data alone, however, cannot be relied upon to infer the degree of past and present competition as Adams and Tschinkel (1995) found that it might be difficult to infer even when the probability of mortality is shown to depend on local spacing in field experiments. This is because they found that colonies of *Solenopsis invicta* Buren in clumped patterns were more likely to brood (ant eggs, larvae, and pupae) raid neighbors than colonies in regular hexagonal patterns. Hence, crowding increased mortality, but conversely, brood raiding did not increase spatial regularity. In any case, the nesting habits of pavement ants and odorous house ants may make this a challenge, as their nests can, respectively, be difficult to locate and change seasonally.

A more in-depth study of arrival sequences at resources would also elucidate how this dominance hierarchy functions. The abundance of ants was assessed at the bait stations and, thus, can be considered to be more representative of foraging activity rather than colony strength, but the sequence of arrival was not captured in much detail. Barbieri et al. (2013) looked at interspecific competition in terms of arrival sequences and how this changes with diet in *Prolasius advena* Frederick Smith and *Monomorium antarcticum* Frederick Smith. A study involving different baits reflecting the preferences of the species involved in our study would be revealing.

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