

Seasonal polydomy in a polygynous supercolony of the odorous house ant, *Tapinoma sessile*

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Abstract. 1. The odorous house ant, *Tapinoma sessile*, is a native ant species common throughout North America. In its natural habitat, *T. sessile* is a low-key species that consists of small colonies. In invaded urban areas, *T. sessile* exhibits extreme polygyny and polydomy and becomes a dominant invasive pest.

2. The current study examined: (i) the density, persistence, and the spatial distribution of nests in a large supercolony of *T. sessile*, (ii) trail abundance and overall colony connectivity as facilitated by the network of trails, (iii) the abundance and the spatial distribution of competing ant species, and (iv) the effect of environmental factors on the number and distribution of *T. sessile* nests.

3. A distinct pattern of seasonal polydomy was observed, whereby the colony undergoes an annual fission-fusion cycle. The colony occupies one or a few nests during the winter, experiences rapid exponential growth in the spring to colonize available nesting sites, reaches maximum nest density in the summer, and again coalesces in the winter, returning to the same winter location year after year. The trails show spatio-temporal variation as well, depending on the location of nesting and foraging sites. Furthermore, nest movements may be driven by soil microclimate and proximity to man-made structures.

4. In total, 119 ant nests were discovered in a 3.15 ha plot, 90 (76%) of which belonged to *T. sessile*. *Tapinoma sessile* exhibited strong colony connectivity as 78/90 (87%) of nests were connected to at least one other nest by a trail. Mean persistence time for *T. sessile* nests was 133 ± 5 days.

5. Results indicate that *T. sessile* is a highly adaptable native ant species that exhibits a high degree of flexibility in its colony social structure. A high degree of polygyny and polydomy may contribute to its ecological dominance and pest status in urban environments.

Key words. Invasive ants, nest persistence, odorous house ant, polygyny, seasonal polydomy, supercolony, *Tapinoma sessile*.

Introduction

Ant colonies function at various organisational levels, ranging from colonies that occupy only one nest (i.e. monodomy) to colonies that occupy multiple nests, a condition known as polydomy (reviewed in Debout *et al.*, 2007). In polydomous colonies, nests are separated spatially, but connected socially by the exchange of workers, queens, brood, and food. As individuals migrate among nests, the colonies also exchange genetic mate-

rial which should ideally result in genetic homogeneity. However, studies suggest that genotypes often tend to cluster in space (Herbers & Grieco, 1994; Beye *et al.*, 1997; Pirk *et al.*, 2001). Polydomy is frequently associated with polygyny (Rosengren & Pamilo, 1983; Ross & Fletcher, 1985; Keller, 1991) suggesting that similar evolutionary forces may favour both traits. However, polydomy is not a consequence of polygyny (Hölldobler & Wilson, 1977) and many monogynous and polydomous species are known (reviewed in Debout *et al.*, 2007). On a larger scale, polydomy appears to be an extremely labile feature and does not seem to be linked to any specific set of ecological or social conditions (Debout *et al.*, 2007). It has evolved numerous times independently and is present in all the

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main subfamilies of ants (Debout *et al.*, 2007). Among species in which polydomy has been recorded, it is a facultative trait in 84% of species (Debout *et al.*, 2007). Polydomy is also frequently a characteristic associated with invasive ant species, most notably *Wasmannia auropunctata* (Clark *et al.*, 1982), *Linepithema humile* (Tsutsui & Case, 2001; Giraud *et al.*, 2002; Buczkowski *et al.*, 2004), and *Solenopsis invicta* (Passera, 1994). Furthermore, experimental studies on invasive ants demonstrate that polydomy can promote high worker numbers and provide advantages in exploitative and interference competition (Human & Gordon, 1996; Holway *et al.*, 1998; Holway & Case, 2000; Heller & Gordon, 2006).

Polydomy appears to confer unique ecological advantages, and approximately half of all polydomous species examined to date can be characterised as ecologically dominant (Debout *et al.*, 2007). A variety of ecological factors may favour a polydomous colony structure. First, polydomous colonies may reduce the costs of foraging by engaging in dispersed central-place foraging, whereby colonies redistribute workers, queens, and brood among nests in response to the spatiotemporal heterogeneity of food resources (McIver, 1991; Holway & Case, 2000; Buczkowski & Bennett, 2006). Such foraging strategy maximises the net energy yield by reducing food transport costs (Orians & Pearson, 1979; Stephens & Krebs, 1986) and may also help defend food sources from competitors. Moreover, Greenslade (1974) demonstrated that polydomous colonies are more efficient at collecting resources in habitats with low productivity. Polydomy can also have other adaptive benefits, including increased colony survival in case some nests are destroyed (Rosengren & Pamilo, 1983; van Wilgenburg & Elgar, 2007a), improved thermoregulation and possibly increased brood production (Banschbach *et al.*, 1997). While polydomy offers many ecological and evolutionary advantages, it also creates a number of challenges for social insect colonies. One major challenge is the need to recognise individuals from distant nests. As nests become spatially diffuse, chemical communication between individuals diminishes and individuals may develop localised *gestalt* odours (van Wilgenburg *et al.*, 2006). This is possibly a result of utilising distinct food and nesting resources, which have been shown to play an important role in nest-mate recognition (Vander Meer & Morel, 1998; Liang & Silverman, 2000). To maintain colony integrity, workers and cuticular hydrocarbons are exchanged among nests (Dahbi *et al.*, 1997; Dahbi & Lenoir, 1998). The presence of spatially separate groups may also lead to a queen-worker conflict over sex allocation and other allocation decisions (Snyder & Herbers, 1991; Backus, 1993; Herbers *et al.*, 2001). Furthermore, polydomy may lead to increased predation as individuals, especially brood, are moved among nests.

Occasionally, polydomy may be a seasonal phenomenon (reviewed in Debout *et al.*, 2007) whereby the colony overwinters in one nest, fractionates into a number of units during the active season, and again coalesces into a single unit at the end of the season. Although seasonal polydomy has been described in several species (Alloway *et al.*, 1982; Rosengren *et al.*, 1985; Snyder & Herbers, 1991; Dillier & Wehner, 2004; Elias *et al.*, 2005; Heller & Gordon, 2006) it is relatively rare, and has been demonstrated in only 10% of polydomous

species (Debout *et al.*, 2007). Seasonal polydomy, by its very nature, is associated with frequent nest movement as the colonies migrate from winter nest(s) to summer nests. Such high vagility poses a number of special challenges for the colony. First, scouts must locate a suitable nest site and recruit nest mates to move. The colony must be moved safely to avoid predation or desiccation. A new nest must be built, which might involve competition for space and food resources with other species (Traniello & Levings, 1986; Wiernasz & Cole, 1995; McGlynn *et al.*, 2004). Furthermore, building a nest is probably a considerable energy expenditure for species that construct nests rather than utilise existing cavities. Yet, despite these factors, ant colonies move frequently (Herbers, 1989; Hölldobler & Wilson, 1990; Banschbach & Herbers, 1999; Gibb & Hochuli, 2003; McGlynn *et al.*, 2004; Backus *et al.*, 2006; Heller & Gordon, 2006). Nest movement also creates problems for those who study the spatiotemporal patterns of nest distribution in ant colonies. First, it is difficult to differentiate inactive nests from those that have been abandoned. Under field conditions, it is also extremely difficult to track the fate of nests, to determine whether they became extinct, moved to a new location, or became assimilated by a neighbouring nest. True nest movement must be distinguished from simple shifts in worker and brood concentrations. Also, due to disturbance, nest movement must be distinguished from a seasonal nest movement. Nest observations may induce relocation behaviour, and demographic censuses on a single nest can only be performed once before the nest is disturbed. Furthermore, numerous biotic and abiotic factors may influence nest relocation, often with synergistic effects that may be difficult to tease apart. As a result, the ecology of polydomy remains relatively unexplored (Debout *et al.*, 2007).

To advance our understanding of seasonal polydomy, we assessed temporal and spatial patterns of nest distribution in the facultatively polydomous and polygynous odorous house ant, *Tapinoma sessile* (Say). The odorous house ant is a native species common throughout North America. In urban areas it is classified as a pest species (Thompson, 1990) and exhibits several attributes characteristic of an invasive tramp species (*sensu* Passera, 1994). These include extreme polygyny, colony reproduction by budding, no internest aggression, generalist diet, polydomy, and ecological dominance in invaded areas. *Tapinoma sessile* is very opportunistic and inhabits a variety of nesting sites, both natural and man-made. The nests are usually shallow, in mulch or debris, or protected inside structures. Previous studies reported that colonies of *T. sessile* move on a regular basis. For example, Smallwood and Culver (1979) reported that 78% of *T. sessile* nests in a temperate forest changed location within 21 days. In a laboratory study, Meissner and Silverman (2001) reported that *T. sessile* moved nests depending on the attractiveness of the nesting substrate. Previously, we examined the ecology of foraging and the pathways of food distribution in a large supercolony of *T. sessile*, and discovered that *T. sessile* are dispersed central-place foragers, whereby ants from individual nests travel along well-established trails, exhibit high foraging site fidelity, and forage on a local scale (Buczkowski & Bennett, 2006). Thus, this population is discontinuous, at least with respect to foraging.

This population also appears to be seasonally polydomous with one or a few overwintering nests and numerous summer nests. In the current study, we examine the density, persistence, and the spatial distribution of nests in this large supercolony of *T. sessile*. We also examine trail abundance and overall colony connectivity as facilitated by the network of trails. Finally, we examine the effect of environmental factors on the number and distribution of *T. sessile* nests.

Methods

Study site

The study site was a 210 x 150 m (3.15 ha) plot on the campus of Purdue University, West Lafayette, IN (Fig. 1). This habitat is a managed urban landscape and contains buildings, sidewalks, and landscaping, including numerous trees and shrubs, mulched areas, and lawns. The site is occupied by a large polydomous supercolony of *T. sessile*, which consists of numerous nests and an extensive network of trails (Buczkowski & Bennett, 2006). The nests belong to one supercolony, as was evidenced by lack of intra-specific aggression among even the most distant nests (Buczkowski & Bennett, 2006). Examination of areas extending approximately 100 m in each direction beyond what is presented in Fig. 1, revealed the presence of numerous ant species, but no *T. sessile*. Queen and worker voucher specimens were deposited in the Purdue Entomological Research Collection at Purdue University.

Nest density, spatial distribution, persistence, and competing species

Spatiotemporal nest distribution was assessed by dividing the study plot into 35 30 x 30 m quadrants (Fig. 1) and exhaustively searching each plot for visual signs of ant trailing activity, inspecting debris on the ground (mulch, leaves, rocks, etc.) with minimal disturbance, or following workers from baits (jelly) back to their nests. *Tapinoma sessile* nests are easily sampled as they are shallow in mulch, pine straw, or other debris on the ground and are easily examined without alarming the workers. In 2007, *T. sessile* activity was first observed on 21st March, nest mapping began on 23rd March, and all 35 quadrants were sampled approximately bi-weekly until 2nd November, when ant seasonal activity drastically declined as a result of low nightly temperatures. In total, each quadrant was inspected 17 times during the 8-month span. Once a nest was discovered, it was mapped and all mapped locations were re-inspected at all subsequent visits. This allowed us to map all nests as either new or persisting from a previous survey, and allowed us to track the temporal distribution and persistence of nests. Three variables were created to measure the frequency of nest relocation. The first variable, relocation frequency, was the number of relocation events divided by the number of observation events. The second variable was nest persistence, calculated as the number of inspections when a nest was present divided by the total number of inspections from the time the nest first appeared, until

the end of the season. The third variable was simply duration of nest occupation, defined as the number of days a nest was active plus 7 days (Braschler & Baur, 2003). In addition to searching for *T. sessile*, other ant species were also identified and mapped. This was accomplished by searching all quadrants for visual signs of ant nesting or foraging activity, inspecting debris on the ground (mulch, leaves, rocks, etc.), or following workers from baits (jelly) back to their nests. Finally, we examined whether the increase in nest abundance in the spring, before the summer maxima, fit an exponential growth curve. This was accomplished by a linear regression on the logarithm of nest count values over time.

Trail abundance, length, and traffic

In addition to mapping nests, the patterns of worker and brood movement were also examined by observing ant trailing activity and mapping all major trails. *Tapinoma sessile* travel along well-established trails and exhibit high trail fidelity (Buczkowski & Bennett, 2006). The trails connect the nests to food resources, but also serve as avenues for the exchange of workers, queens, and brood among the distant nests. The trails are usually clearly visible, as the ants prefer to use physical guidelines (e.g. walls, tree branches) to facilitate the movement of resources. Seven major trails (Fig. 1 and Table 1) were selected and the intensity of foraging activity on each trail was estimated by counting the number of workers that crossed an imaginary line on the trail in 1 minute. This was repeated for each trail at each of the 17 inspection dates. The most active and permanent trails were chosen to maximise the chance of observing ants on each inspection day, and some of the trails used in this study were the same as those used by Buczkowski and Bennett (2006). If the direction of the trail changed slightly or minor temporary side trails were added, it was still considered the same trail. Ant activity was estimated in the early afternoon, between 13.00 and 14.00 hours and three counts were performed for each trail. Colony connectivity was determined for the study plot, by examining the percentage of nests connected by a trail to other nests.

Environmental factors

The effect of environmental factors on the abundance of *T. sessile* nests, was estimated by examining the relationship between the number of nests on each sampling date and air temperature, bare soil temperature, and air humidity, all recorded at 14.00 hours. Furthermore, the relationship between the number of nests and the number of woody plants in each of the 35 quadrants was examined. Woody plants were considered all trees and shrubs that could potentially harbour honeydew-producing Hemiptera, regardless of size. The effect of other vegetation (e.g. lawns) was not considered, because preliminary observations indicated that *T. sessile* almost never nested in grassy areas, perhaps due to the fact that *T. sessile* do not construct nests, but rather prefer to nest in existing cavities in protected areas.

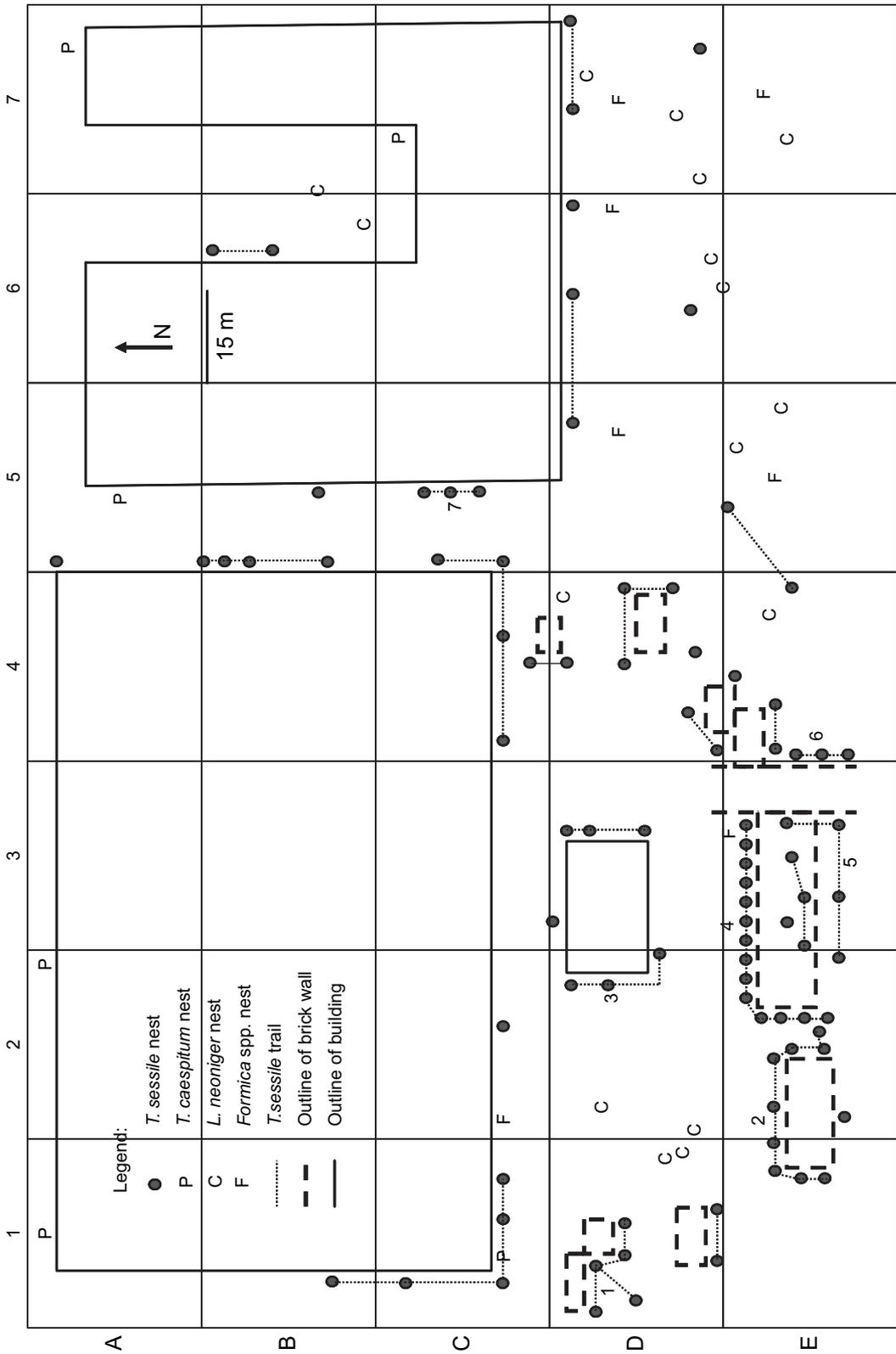


Fig. 1. Schematic diagram, drawn to scale, showing the spatial distribution of *Tapinoma sessile* nests. All 90 nests discovered during the study are indicated. Numbers next to foraging trails indicate trails used to study foraging patterns.

Table 1. Ant trailing activity and nest density on seven major trails observed in the study plot.

Trail number	Trail length (m)	Average ant count per minute	Range in ant activity	Number of nests on the trail
Trail 1	35	38 ± 6	0–78	5
Trail 2	37	88 ± 15	2–165	9
Trail 3	22	55 ± 11	0–122	3
Trail 4	48	84 ± 14	14–175	14
Trail 5	32	49 ± 9	0–103	4
Trail 6	12	91 ± 14	0–184	3
Trail 7	10	40 ± 8	0–105	3
Mean ± SEM	28 ± 5	64 ± 9		6 ± 2

Data analysis

All data analyses were performed using SAS 8.1 statistical software (SAS Institute, 2002) on means derived by averaging over days within a replicate. PROC REG was used to examine whether early season nest abundance fit an exponential model. The relationship between nest abundance and various environmental factors (air temperature, soil temperature, air humidity) and between trail length and the number of nests on the trail were examined using PROC CORR using Spearman's rank correlation.

Results

Nest density, spatial distribution, persistence, and competing species

Tapinoma sessile activity was first observed on 21st March and nest mapping began on 23rd March, when seven nests were discovered (Fig. 2). From 23rd March until 4th May the total number of nests increased exponentially, showing an almost perfect fit to an exponential curve ($r = 0.994$, $P = 0.003$). The rate of increase in the number of nests was the highest from 5th April to 20th April when the number of nests increased from 12 to 33 (275% increase), and from 20th April to 4th May when the number of nests increased from 33 to 85 (258% increase). After 4th May, the number of nests remained steady for approximately the next 14 weeks, or until August 11th. The number of nests began to gradually decline after August 11th and few nests were observed after the first week of November. The supercolony of *T. sessile* occupied a total of 90 different nesting sites (shown in Fig. 1). The nests reached the greatest density on 16th May and 16th June when 87 out of 90 nesting locations were utilised. Nest density ranged from 0 to 14 nests per quadrant and mean nest density was 2.5 ± 0.6 nests per quadrant (Fig. 1). *Tapinoma sessile* was absent in 15/35 quadrants (43%) and no ants were present in 9/35 quadrants (26%).

The average relocation frequency was 0.027 ± 0.005 (range 0–0.21). Mean nest persistence was $70\% \pm 2$ and ranged from 14 to 100%. Five out of 90 nests (6%) were present during all 17 inspections. Mean persistence time for *T. sessile* nests was 133 ± 5 days.

In total, 119 ant nests were discovered at the study site. Of those, 90 (76%) belonged to *T. sessile*, while the remainder was shared among three other ant species including cornfield ants, *Lasius alienus* (16 nests, 13%), pavement ants, *Tetramorium caespitum* (six nests, 5%), and field ants *Formica* spp. (seven nests, 6%). The spatial nest distribution for all species is indicated in Fig. 1.

Trail abundance, length, and traffic

The study site contained a large number of foraging trails of various lengths, and the number, direction, and intensity of the trails varied throughout the test period (March–November). However, other trails remained consistently utilised throughout the season, as they were associated with attractive nesting sites and/or permanent feeding sites. All major foraging trails are indicated in Fig. 1 (trails 1–7) and are further characterised in Table 1. Mean trail length was 28 ± 5 m and ranged from 10 m (Trail 7) to 48 m (Trail 4). The mean number of ants moving along the trails was 64 ± 9 ants per minute and ranged from 38 to 91 ants per minute. The mean number of nests on the trails was 6 ± 2 (range 3–14). Trail length and the number of nests on the trail were significantly correlated ($r = 0.837$, $P = 0.0005$). However, there was no correlation between the number of nests on the trail and the average ant traffic ($r = 0.522$, $P = 0.875$). In contrast to the more transient trails, the overall length of permanent trails changed very little during the season. That is, the ants added new nests along existing trails (thus increasing local nest density), rather than extending the trails to accommodate new nests. *Tapinoma sessile* exhibited strong colony connectivity as 78 out of 90 (87%) nests in the study plot were connected to at least one other nest by a trail. Of the 90 nests discovered, only 11 were solitary (comprising 12% of total nests; Fig. 1). The remaining nest groupings were: eight nest pairs (18%), six nest triples (20%), three nest quadruplets (13%), two groups of five nests (11%), one group of nine nests (10%), and one group of 14 nests (16%). This indicates that most nests were connected to few other nests, while some areas may harbour dense aggregations where nest density and social connectivity are high.

Environmental factors

The number of *T. sessile* nests in the study plot increased as the season progressed and mean daily air temperature increased. However, no relationship between air temperature on a given day and the number of nests on that day was detected ($r = 0.419$, $P = 0.090$). This is most likely due to the fact that the number of nests remained steady throughout the summer (from May until August), despite relatively large fluctuations in air temperature, and the number of nests began to decline in late summer despite relatively steady high temperatures. Overall, the number of nests increased exponentially from 23rd March to 4th May, a time when the mean daily air temperatures were still relatively low. The number of nests remained relatively steady throughout the summer (from May until August) and began to decline in late summer (September). Likewise, no relationship

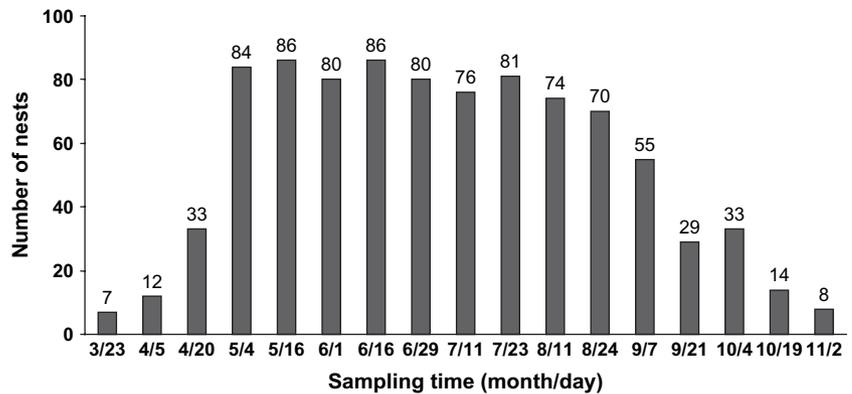


Fig. 2. Seasonal abundance of *Tapinoma sessile* nests in the study plot. Numbers above bars indicate the number of active nests present in the study plot.

between air humidity on a given day and the number of nests sampled on that day was detected ($r = -0.269$, $P = 0.296$). Air humidity varied greatly, even when the number of nests did not, and it is likely that soil moisture content influenced nest abundance and distribution to a greater extent. A significant positive relationship between soil temperature and nest abundance was detected ($r = 0.630$, $P = 0.006$), suggesting that *T. sessile* nests may fractionate as soil temperature increases, possibly because warmer soil may provide optimal conditions for the developing brood. A total of 350 woody plants were identified in the study plot and the mean woody plant density was 10 ± 2 (range 0–65). No relationship between woody plant density and ant nest density was detected, even when only quadrants that actually contained *T. sessile* were included in the analysis. Numerous quadrants contained woody plants, but no ant nests, possibly because the quadrants lacked other environmental characteristics preferred by the ants (e.g. buildings, mulch beds) or were on the periphery of the supercolony.

Discussion

Seasonal polydomy is a relatively rare phenomenon, having been observed in only 10% of polydomous ant species (Debout *et al.*, 2007) and little is known about the adaptive significance of seasonal polydomy (Banschbach *et al.*, 1997). Polydomy has often been considered a response to various environmental constraints, including colony extinction as a result of predation (Rosengren & Pamilo, 1983; van Wilgenburg & Elgar, 2007a), variation in patch quality with the territory (Pfeiffer & Linsenmair, 1998; van Wilgenburg & Elgar, 2007b), constraints on nest size and placement (Levings & Traniello, 1981), and thermoregulation (Banschbach *et al.*, 1997). Results from our study demonstrate distinct seasonal polydomy in *T. sessile*, which involves a seasonal shift in nest abundance and location. The colony overwinters in a central location (as one or a few nests), rapidly disperses in the spring to colonise available nesting sites, reaches maximum nest density in the summer, and again coalesces in the winter, returning to the same winter location year after year. Based on annual observations performed over the past 4 years, the overwintering location is building in

quadrants D2–3. Every year, this is where activity is last seen in the fall and first seen in the spring. As a result of nest expansion, new trails are also established. Observations indicate that early in the season (March–April), *T. sessile* maintained few trails and mainly used trails to colonise new areas. Workers were frequently observed moving brood (including clumps of eggs) along the trails and queens migrated as well. As the season progressed and plants within the study plot became colonised with honeydew-producing Hemiptera, *T. sessile* established additional foraging trails to attractive feeding sites, and frequently nested at the base of plants. Colonisation of new areas by *T. sessile* is most likely a stepwise process, whereby the most distant summer nests (e.g. quadrants A5, B6, D7) are not colonised directly from the winter nest, but rather through a series of intermediate summer nests. The capability of *T. sessile* to experience an enormous early-season population growth, is evidenced by the fact that the number of nests grew exponentially from 23rd March to 4th May. The increase in actual workers counts (not estimated in this study) was probably even more impressive. Such fast colony expansion is especially remarkable given that early season night temperatures at our study site were frequently close to freezing and food was scarce, as honeydew-producing Hemiptera were not yet present. However, the actual percentage of workers that survive the winter is unknown and therefore, it is difficult to determine the degree to which the supercolony increased in numbers, as opposed to simply becoming active again. Future studies should focus on estimating the percentage of the workers that survive the winter in order to determine the proportion of workers that are produced anew each spring, versus those that simply resume activity.

The distribution of nests in a polydomous colony may be affected by many factors, such as the patchiness of food resources, distance between patches, nest site availability, and pressure from competing species. In our study, nest placement in *T. sessile* was driven by proximity to human-made structures and soil microclimate. *Tapinoma sessile* occupied a relatively large area with abundant nesting sites and a large number of Hemiptera-infested trees and shrubs, which provided stable, local food resources. Based on the observed nest distribution pattern, it appears that the major factor driving the distribution of *T. sessile* nests in urban environments, is the proximity to man-made

structures. Man-made structures offer protection from fluctuations in outdoor conditions, protection from possible predators, a place to incubate brood, and access to human food. Therefore, it appears that the spatial distribution of available nesting sites affected the distribution of nests in *T. sessile* and dictated the observed foraging pattern, i.e. the ants colonised the most attractive nesting sites and then utilised the closest available food source. Nesting in open areas, such as lawns, was never observed in *T. sessile* and the ants avoided trailing through open areas. They mainly utilized structural guidelines when moving between nests. Similarly, *T. caespitum* usually nested in close proximity to buildings and usually excavated their nests underneath concrete slabs. This is in contrast to the other two species, *L. alienus* and *Formica* spp. which almost always excavated nests in open areas, usually lawns or patches of bare soil. *Tapinoma sessile* nests were relatively stable as indicated by the low relocation frequency (0.027 ± 0.005) and relatively high mean nest persistence of 133 ± 5 days. However, sometimes substantial changes in worker and brood concentrations within active nests were observed, and trailing activity varied greatly as well (Table 1). Odorous house ants moved nests in response to adverse conditions. However, nests appeared to be moved between fixed locations, that is, abandoned nesting locations frequently became re-colonised as the conditions improved again. On the one hand, the supercolony appears to have very strong social connectivity as 78 out of 90 (87%) of *T. sessile* nests were connected to at least one other nest by a trail. On the other hand, the colony is disjointed as food distribution in the colony is extremely localised (Buczkowski & Bennett, 2006). This was indicated by the fact that *T. sessile* from different nests forage on a local scale (dispersed central-place foraging), distribute harvested resources locally (i.e. only along foraging trails where food was found, but not between foraging trails), and exchange few or no workers with nests not directly connected by a trail (Buczkowski & Bennett, 2006). Woody plants did not affect the distribution of nests, even though the ants usually nested in debris at the base of trees (e.g. mulch, pine needles) and woody plants were attractive to *T. sessile* for a number of reasons. First, woody plants harboured honeydew-excreting Hemiptera and were thus highly attractive foraging sites. Second, woody plants were usually associated with drip irrigation, which provided moisture during the summer months. Finally, trees and shrubs were usually surrounded by mulch beds, which provided attractive nesting refugia. Another factor that regulated the expansion of *T. sessile* nests was soil temperature. The number of nests increased with increasing soil temperature, suggesting that *T. sessile* nests may fractionate as soil temperature increases, possibly because warmer soil may provide optimal conditions for the developing brood. Soil temperature also influenced the distribution of nests in the Argentine ant (Heller & Gordon, 2006).

In many respects, the life history and behavioural traits of *T. sessile* are similar to those found in introduced invasive species, especially the Argentine ant, *Linepithema humile*. *Tapinoma sessile* may be highly polygynous, polydomous, and can attain enormous population sizes, much like the invasive *L. humile* (Markin, 1970). *Tapinoma sessile* show seasonal polydomy, which had also been documented in *L. humile* (Heller & Gordon, 2006). Heller and Gordon (2006) reported that *L. humile* showed

a highly predictable annual fission-fusion cycle, whereby the nest size, abundance, and location varied in similar ways across sites and years. In invaded urban environments, *T. sessile* may also negatively affect the abundance and diversity of native ant species, as has been demonstrated for *L. humile* (Holway, 1999; Human & Gordon, 1999). *Tapinoma sessile* coexisted with only three additional ant species at our study site. Comparative data from other plots with similar landscape characteristics, and the absence of *T. sessile* indicates a higher number of ant genera, including *Camponotus*, *Crematogaster*, *Monomorium*, and *Solenopsis* (G.B., pers. obs.). Interestingly, *T. sessile* appears to have a negative affect on arboreal ants including *Crematogaster cerasi* and various *Camponotus* species. It is possible that arboreal ant species were deterred from nesting and/or foraging on trees where large numbers of *T. sessile* actively foraged. Recent work indicates that *T. sessile* can effectively compete with other ants, including the invasive Argentine ant (Buczkowski & Bennett, 2008). *Tapinoma sessile* are aggressive fighters and frequently outcompeted *L. humile* in one-on-one interactions. However, *T. sessile* lost to *L. humile* in group fights and a resource competition assay (Buczkowski & Bennett, 2008). Additional work will be necessary to fully document the impact of *T. sessile* on other ant species.

Tapinoma sessile were clearly ecologically dominant at the study site, as 76% of all nests discovered belonged to *T. sessile*. However, we estimate that in terms of the biomass and individual ant counts, *T. sessile* comprised > 99% of all ants present. Furthermore, the geometric distribution typically characterises communities where a single resource is exploited by the community, and one abiotic factor has a very large effect on a species' success. In our study site, human-provided refugia appeared to be heavily utilised by *T. sessile* (Fig. 1) and their availability most likely played a major role in the success of *T. sessile*. *Tapinoma sessile* is a unique native ant species, in that it displays an extreme flexibility in colony social structure and tends to become invasive when given the opportunity. In natural habitats (e.g. mature hardwood forests of Ohio and Indiana), *T. sessile* colonies are strictly monogynous and have relatively few workers (approx. 15–100; G.B., pers. obs.). The ants nest in above-ground cavities (e.g. acorns, sticks), most likely face fierce competition from other forest-dwelling ants, and are never the dominant species (Smallwood & Culver, 1979; Herbers, 1989; Holway, 1999; Human & Gordon, 1999). In contrast, *T. sessile* in disturbed urban habitats are highly polygynous and polydomous, reach large colony size, seem to easily outcompete other ant species, and become serious nuisance pests (Thompson, 1990). Such extreme flexibility in social structure offers a unique opportunity to study the evolution of polydomy. Specifically, a comparison of monogynous and monodomous colonies with polygynous and polydomous colonies would allow us to distinguish between life-history traits that have evolved as a result of adopting a polydomous lifestyle.

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