The Effects of Colony Structure and Resource Abundance on Food Dispersal in Tapinoma sessile (Hymenoptera: Formicidae)

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RESEARCH

The Effects of Colony Structure and Resource Abundance on Food Dispersal in *Tapinoma sessile* (Hymenoptera: Formicidae)

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ABSTRACT. The odorous house ant, *Tapinoma sessile* (Say) (Hymenoptera: Formicidae), exhibits a high degree of variation in colony spatial structure which may have direct and indirect effects on foraging. Protein marking and mark–release–recapture techniques were utilized to examine the effect of colony spatial structure on food dispersal. Sucrose water spiked with rabbit IgG protein was presented to colonies with varying spatial configurations in laboratory and field experiments. In monodomous lab colonies, the rate and extent of food dispersal was rapid due to a decrease in foraging area. In polydomous colonies, food dispersal was slower because conspecifics were forced to forage and share food over longer distances. However, over time, food was present in all extremities of the colony. Experiments conducted in the field produced similar results, with nests in close proximity to food yielding higher percentages of workers scoring positive for the marker. However, the percentage of workers possessing the marker decreased over time. Results from this study provide experimental data on mechanisms of food dispersal in monodomous and polydomous colonies of ants, and may be important for increasing the efficacy of management strategies against *T. sessile* and other pest ant species.

Key Words: foraging, odorous house ant, immunomarking, polydomy, food dispersal

In numerous species of social Hymenoptera, individuals within the colony occupy a single nest, a condition known as monodomy. This single-nest configuration induces centralized foraging whereby individuals disperse from the nest in search of food and other resources (Traniello 1989). In contrast to this social configuration, other species live in polydomous colonies consisting of nests which are separated spatially yet connected socially by the exchange of individuals and resources (Rosengren and Pamilo 1983). The evolution of polydomy is thought to be a direct consequence of polygyny, the condition where a colony possesses multiple reproductives (Hölldobler and Wilson 1977, Rosengren and Pamilo 1983). As colonies produce newly mated queens, dispersal of these queens can occur to form connected, outlying nests in proximity to the original nest, thus establishing a polydomous colony. Workers from separate nests within polydomous colonies may engage in cooperative behaviors such as foraging and brood care (Hölldobler and Lumsden 1980, Holway and Case 2000). As opposed to centralized foraging in monodomous colonies, polydomous colonies engage in a less uniform method of foraging which allows for the localized acquisition of food among individual nests, eliminating the need to return to the focal nest (Hölldobler and Lumsden 1980, McIver 1991, Buczkowski and Bennett 2006). This multinest configuration allows colonies to redistribute nests in response to the ever-changing distribution of food and resources (Hölldobler and Lumsden 1980, McIver 1991, Holway and Case 2000). Previous research also suggests that lessened intraspecific aggression has led to increased interspecific competitive prowess, which in turn is thought to have positively influenced the ecological success of other polydomous ant species such as the Argentine ant, *Linepithema humile* (Mayr) (Human and Gordon 1996, Holway and Case 2000) and the odorous house ant, *Tapinoma sessile* (Say) (Hymenoptera: Formicidae) (Buczkowski 2010, Menke et al. 2010).

Ants utilize trophallaxis, the process of exchanging gut contents via regurgitation, as a means of food transfer. Trophallaxis occurs between all castes within a colony and is necessary for those which cannot feed directly (Wilson 1971). Aside from serving as a means to exchange food from one nestmate to another, trophallaxis allows ants to exchange cuticular hydrocarbons (Boulay et al. 2000) and glandular secretions (Markin 1970a). Thus, food exchange in ants is believed to have been influential in the evolution of social behaviors (Choe and Crespi 1997). Before the process of food exchange can be initiated, foragers must first disperse from the colony in search of food. These foragers, generally members from the worker caste, forage as a cooperative unit, utilizing chemically-mediated trails to locate and direct other workers towards the food source (Hölldobler and Lumsden 1980). Food distribution within the colony is then initiated upon the return of foraging workers.

Previous studies with *T. sessile* (Buczkowski and Bennett 2006, 2009) suggest that colony spatial structure plays a crucial role in food distribution. Evidence from field studies shows that *T. sessile* forage locally with limited food exchange among nearby nests (Buczkowski and Bennett 2006). In addition to *T. sessile*, other polydomous ant species such as *L. humile* provide little investment in the construction of nests (Newell and Barber 1913, Markin 1970b), suggesting that food location influences both colony structural design through nest distribution and foraging strategy (Holway and Case 2000). The spatial distribution of nests can affect both the acquisition of food via foraging as well as the rate of trophallactic exchange among workers. Other studies demonstrate a negative relationship between food flow and colony size (Buczkowski and VanWeelden 2010). While maintaining consistent foraging space but increasing colony size, fewer workers displayed evidence of feeding due to the limited food supply and clustered allocation of workers. In addition to colony spatial structure, variability in colony size can influence distribution of food in odorous house ants (Buczkowski and Bennett 2009). In experiments where food quantity was held constant, highly populated colonies were able to distribute the food across a greater number of individuals but at a lower per capita rate (Buczkowski and Bennett 2009). Though previous studies have examined the food flow in polydomous ants, data is lacking on the influence of colony structure and relative food location as direct factors in food dispersal.

The objective of this study was to examine the effect of colony structure and resource abundance on food dispersal in the facultatively polydomous *T. sessile*. The study investigated the effect of nest location relative to the food sources on the rate and the extent of food dispersal

throughout the colony. Laboratory experiments were conducted to examine the basic mechanics of food dispersal in colonies of *T. sessile* without the effects of weather, predation, and competition among other colonies. Next, a series of field experiments was conducted to apply techniques from the laboratory experiments to determine if differences in food dispersal rates exist across varying resource densities.

Materials and Methods

Test Species. *T. sessile* is a widespread species native to North America (Fisher and Cover 2007) and is found throughout a variety of natural and urban habitats. Colonies can vary greatly in size and social structure, ranging from small, single-nest monogyne colonies in natural areas to large, multinest, polygyne supercolonies in urban areas (Buczkowski 2010). Laboratory colonies were collected from a previously surveyed supercolony on the campus of Purdue University, West Lafayette, Indiana (Buczkowski and Bennett 2008). Debris containing the ants was returned to the lab and placed into Fluon-coated (Bioquip Products Inc., Rancho Dominquez, CA, http://www.bioquip.com) plastic trays provided with moist plaster nests. As the debris dried, ants colonized the plaster nests which were subsequently transferred to debris-free trays. Colonies were reared on artificial diet (Bhatkar and Whitcomb 1970) and 30% sucrose water ad libitum. Colonies were maintained at 26 ± 2°C, 60 ± 10% relative humidity, and a 12:12 (L:D) h cycle.

Laboratory Feeding Experiments. A series of feeding experiments was conducted to assess the effect of colony structure and resource abundance on food dispersal using experimental colonies of varying spatial configuration. Experimental colonies consisted of three, Fluon-coated, plastic foraging arenas measuring 27 by 20 by 9.5 cm high, arranged in a linear pattern and connected by bridges constructed from thin wooden rods (Fig. 1). Each bridge was built from a 90 cm wooden rod, which was positioned horizontally and connected at each end to a 17-cm vertical support rod, resulting in a 124-cm bridge. Each foraging arena was provided with an artificial nest chamber consisting of a plaster filled-Petri dish and a vial of water. Feeding trials were divided into a three-step process: 1) acclimation, 2) feeding, and 3) sampling. Prior to initiation of each trial, a colony fragment consisting of 1,000 workers, 30 queens, and numerous brood was transferred into each nest chamber and allowed to acclimate without food for 48 h. Following acclimation, 350 µl aliquots of 30% sucrose water spiked with technical grade rabbit IgG protein (Sigma Chemical Co., St. Louis, MO, http://www.sigmaaldrich.com/united-states.html) at 0.5 mg IgG/ml sucrose water were placed into the foraging arenas, and ants were allowed to feed for 1 h. Spiked sucrose water was presented in feeding stations constructed from inverted microcentrifuge tube lids (Fisher Scientific International Inc., Hampton, NH, http://www.fisher.co.uk), allowing for multiple individuals to feed at a single time. After 1 h, remaining sucrose water was removed, and 30 workers and 3 queens were sampled from each nest chamber at 1 and 8 h after initiation of feeding and stored individually in microcentrifuge tubes at −20°C until the enzyme-linked immunosorbant assay (ELISA) procedure could be initiated. Using the previously described methodology, five feeding experiments were conducted using the following colony configurations 1) small, monodomous colonies, 2) large, monodomous colonies, 3) polydomous colonies with a localized food source, 4) polydomous colonies with dispersed food sources, and 5) polydomous colonies exhibiting delayed feeding (Fig. 1a–e). Small, monodomous colonies (Feeding experiment 1) were artificially established by inserting a colony fragment (1,000 workers and 30 queens) and spiked sucrose water into foraging arena A, while excluding arenas B and C from the configuration. Large, monodomous colonies (Feeding experiment 2) were established by inserting 3,000 workers and 90 queens into foraging arena A, while excluding arenas B and C. The quantity of spiked sucrose water was increased to 1.05 ml. Polydomous colonies with a localized food source (Feeding experiment 3) were established by placing a colony fragment (1,000 workers and 30 queens) into each arena, and limiting spiked sucrose water to foraging arena A. Polydomous colonies with dispersed food sources (Feeding experiment 4) were identical to colonies in Feeding experiment 3, except that all foraging arenas were provided with an aliquot of spiked sucrose water. Polydomous colonies subjected to delayed foraging (Feeding experiment 5) were also designed using the same configuration as in feeding experiment 3, except that the bridges connecting each foraging arena were removed during the feeding period and reinserted 1 h after feeding. The goal of this feeding experiment was to restrict direct feeding from the food source to ants in foraging arena A, with the intent that they would transport food to foraging arenas B and C following reinsertion of the bridges. All experiments were replicated five times using new colony fragments.

Field Feeding Experiments. To further assess the effect of resource abundance on food dispersal in *T. sessile*, an additional set of feeding experiments was conducted in the field. Experiments were initiated on 28 April 2010 using previously surveyed polydomous *T. sessile* colonies at Purdue University (Buczkowski and Bennett 2008). Spatially separated colonies, each consisting of four interconnected nests, were selected for the feeding experiments. Nest entrances within each colony were organized in a linear configuration along concrete walls, and trails between nests were approximately 260 cm in length. Experiments were replicated three times using separate colonies. Ants were subjected to a similar feeding regime as described in the laboratory experiments, where nests entrances were provided with 5 ml aliquots of 30% sucrose water containing 0.5 mg IgG/ml sucrose water. Ants were allowed to feed for 2 h and 20 workers were collected at each nest 2, 8, and 24 h after feeding. Three feeding experiments were conducted using the following food arrangements : 1) localized food source, 2) dispersed food sources, and 3) food delivery via donor (replete) ants. Colonies with localized food sources (Feeding experiment 1) were established by providing spiked sucrose water to a single nest entrance. In colonies with dispersed food sources (Feeding experiment 2), all nest entrances were provided with spiked sucrose water. For colonies fed using donor ants (Feeding experiment 3), a capture–mark–recapture (CMR) procedure was utilized to introduce donor workers into each colony. The CMR procedure was divided into three steps: 1) collection of workers (donors) from each field colony, 2) feeding the donors sucrose solution containing the protein marker, and 3) reintroduction of donor workers back into their respective colonies with subsequent sampling at allotted time intervals. In the initial step, a sample of 500 workers was collected from the entrance to nest 1 in each colony and returned to the lab. Ants were placed into Fluon-coated trays and provided with a moist plaster nest and water. After 24 h, the ants were offered 5 ml of 30% sucrose water containing 0.5 mg IgG/ml sucrose water, and were allowed to feed ad lib for 2 h. A sample of 300 donor workers was selected from each colony and immediately reintroduced back into their corresponding nests within each field colony. Samples of ants were collected from each nest entrance 2, 8, and 24 h after introduction of donor workers. Individual samples were returned to the lab and stored at −20°C until the ELISA procedure could be performed.

ELISA Procedure. To detect to presence of the IgG marker in the ant gut, samples were analyzed by DAS-ELISA using previously described techniques (Hagler 1997, Hagler and Jackson 1998, Buczkowski and Bennett 2006). Frozen samples were individually homogenized in 150 µl phosphate buffered saline (PBS) (pH = 7.4). Each well of a 96-well microplate was coated with 100 µl of anti-rabbit IgG (Sigma Chemical Co., http://www.sigmaaldrich.com/united-states.html) diluted 1:500 in distilled nanopure water and incubated for 24 h at 4°C. After incubation, the primary antibody was discarded and 300 µl of 1% nonfat dry milk (Bio-Rad Laboratories, Hercules, CA, http://www.bio-rad.com) in distilled nanopure was added to each well to block any remaining nonspecific binding sites. After a 30-min incubation period at 26°C, milk was discarded. Ant samples and five negative control samples (ants exposed to unmarked food) were vortexed, pipetted into the wells of each microplate, and allowed to incubate for 1 h at 26°C. After incubation, the samples were discarded and each well

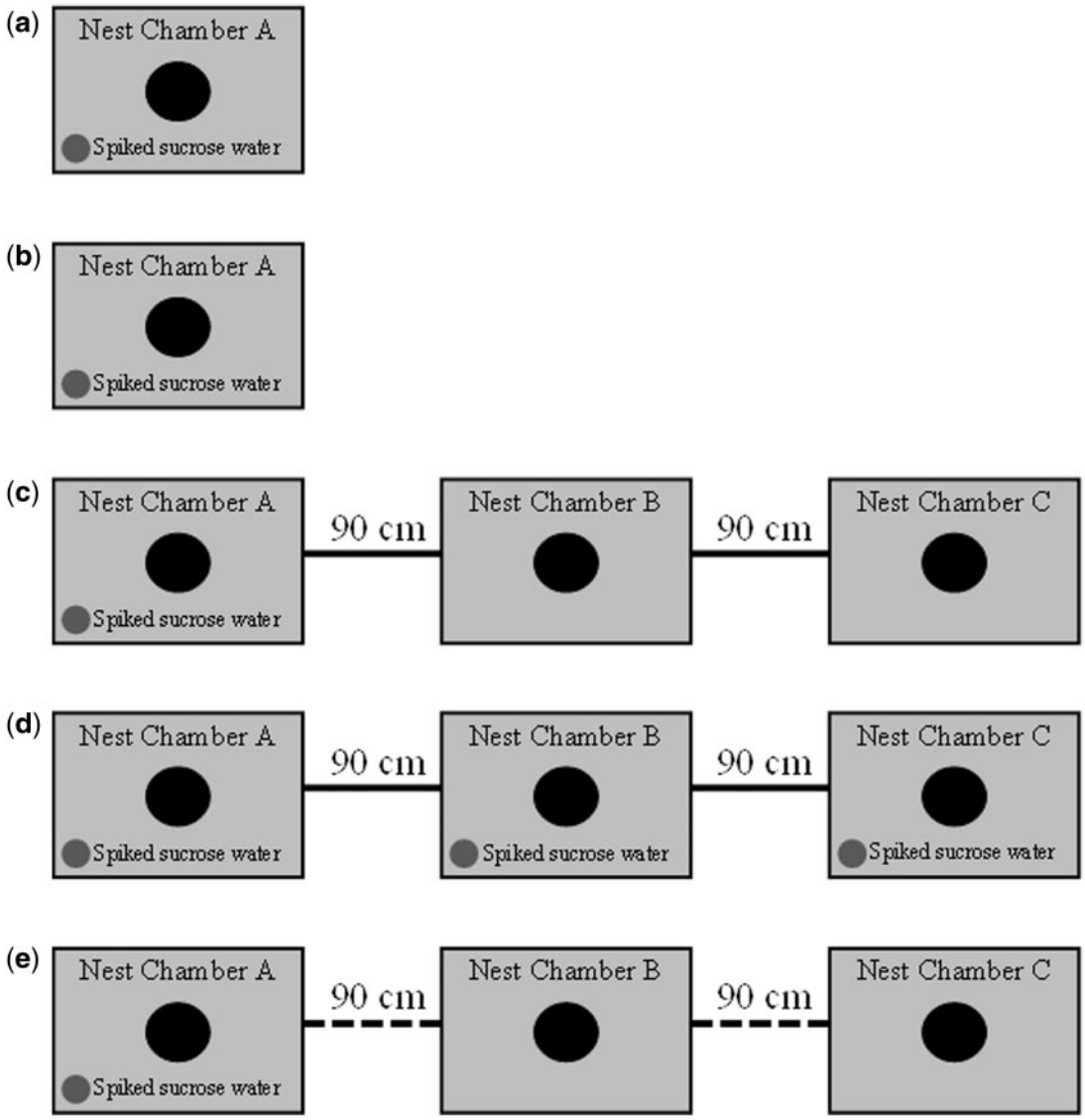

Fig. 1. Laboratory feeding experiment setup (a–e). (a) Feeding experiment 1: monodomous colony, small. (b) Feeding experiment 2: monodomous colony, large. (c) Feeding experiment 3: polydomous colony, localized food source. (d) Feeding experiment 4: polydomous colony, dispersed food source. (e) Feeding experiment 5: polydomous colony, localized food source, delayed foraging. Nest chambers (black, shaded circles) were situated in foraging arenas (27 by 20 by 9.5 cm) connected by wooden bridges.

received three washes of 200 µl PBS Tween (0.05%) and two washes of 200 µl PBS. Next, secondary antibody consisting of antirabbit IgG conjugated to horseradish peroxidase (50 µl) was diluted down to 1:1,000 in 1% nonfat milk, added to each well, and allowed to incubate for 1 h at 26°C. After incubation, the antibody was discarded and the wells were washed again as above. Subsequently, 50 µl of 3,3',5,5'-tetramethylbenzide (TMB) horseradish peroxidase (HRP) substrate (BioFX Laboratories, Owings Mills, MD, http://www.selectscience.net) were added to each well and allowed to incubate for 30 min. Following incubation, microplates were analyzed on a Beckman Coulter AD 340 Absorbance Detector (Beckman Coulter Inc., Brea, CA, www.beckmancoulter.com) at 620 nm, and The mean optical density and the percentage of samples scoring positive for the IgG marker were calculated.

Statistical Analyses. Laboratory and field experiments were analyzed separately. For each experiment, the mean optical density and the mean percent of workers scoring positive for the IgG marker were calculated from each sample. Ants were considered positive for the marker if the optical density was greater than three standard deviations from the mean negative control (0.044) (Hagler et al. 1992, Buczkowski and Bennett 2006). The percentage of ants scoring positive for the marker was calculated for each nest within each colony. Analyses of variance (ANOVAs) were conducted using PROC GLIMMIX (SAS Institute 2008). Food distribution in laboratory experiments was analyzed using three-way ANOVAs with time, nest location, and caste as fixed effects. Random effects for experiments 1 and 2 included replication and caste*replication, while random effects for experiments 3, 4, and 5 included replication, replication*nest location, and replication*nest location*caste. Specific pairwise comparisons were performed to determine differences in the percentage of ants scoring positive between feeding trials 1 and 2, 3 and 4, and 3 and 5. Food distribution in field experiments was analyzed using two-way ANOVAs with time and nest location as fixed effects Random effects included replication and replication*nest location. Tukey's honest significant difference (HSD) test was used for mean separation.

Results

Laboratory Feeding Experiments. In all laboratory experiments, differences were detected in the percentage of ants scoring positive for the IgG marker between castes (Tables 1 and 2), with the rate of food

Table 1. Mean ± SE percentage of *T. sessile* samples scoring positive for the IgG marker, grouped by laboratory feeding experiment

Feeding experiment	Nest	Caste			
		Workers		Queens	
		1 h	8 h	1 h	8 h
1: Monodomous, small	A	79 ± 4 a	87 ± 4 a	47 ± 8 b	60 ± 13 ab
2: Monodomous, large	A	83 ± 2 b	97 ± 1 a	40 ± 3 b	49 ± 15 b
3: Polydomous, localized food source	A	72 ± 9 ab	87 ± 3 a	20 ± 13 cd	7 ± 7 cd
	B	12 ± 5 cd	45 ± 16 abc	0 ± 0 d	0 ± 0 d
	C	14 ± 12 cd	30 ± 11 bcd	0 ± 0 d	0 ± 0 d
4: Polydomous, dispersed food source	A	83 ± 5 a	90 ± 5 a	53 ± 13 a	80 ± 13 a
	B	75 ± 7 a	90 ± 5 a	67 ± 18 a	47 ± 17 a
	C	82 ± 3 a	89 ± 4 a	80 ± 14 a	47 ± 23 a
5: Polydomous, delayed feeding	A	61 ± 10 ab	62 ± 10 ab	67 ± 15 a	13 ± 8 c
	B	___	22 ± 12 bc	___	0 ± 0 c
	C	___	21 ± 17 bc	___	0 ± 0 c

Means are separated by nest location, caste, and time. Means within experiments that are followed by the same letter are not significantly different using Tukey's HSD test ($P < 0.05$).

Table 2. Statistical comparisons of food dispersal in lab colonies of *T. sessile*, measured by nest location, caste and time

Feeding experiment	Fixed Effect	*F*	df	*P* > *F*
1: Monodomous, small	Time	5.15	1.8	0.0524
	Caste	13.88	1.4	0.0204
	Time*caste	0.33	1.8	0.5825
2: Monodomous, large	Time	11.08	1.4	0.0291
	Caste	24.00	1.8	0.0012
	Time*caste	1.17	1.8	0.3100
3: Polydomous, localized food source	Nest location	12.95	2.8	0.0030
	Caste	61.13	1.12	<0.0001
	Nest location*caste	7.67	2.12	0.0072
	Time	4.65	1.24	0.0413
	Time*nest location	1.35	2.24	0.2794
	Ttime*caste	10.87	1.24	0.0030
	Time*nest location*caste	0.42	2.24	0.6611
4: Polydomous, dispersed food source	Nest location	0.23	2.8	0.7971
	Caste	7.08	1.12	0.0207
	Nest location*caste	0.04	2.12	0.9602
	Time	0.01	1.24	0.9364
	Time*nest location	3.76	2.24	0.0379
	Time*caste	4.19	1.24	0.0519
	Time*nest location*caste	4.49	2.24	0.0221
5: Polydomous, delayed foraging	Nest location	25.98	2.8	0.0003
	Caste	9.42	1.12	0.0097
	Nest location*caste	0.60	2.12	0.5656
	Time	0.11	1.24	0.7408
	Time*nest location	6.92	2.24	0.0042
	Time*caste	12.02	1.24	0.0020
	Time*nest location*caste	1.37	2.24	0.2725

dispersal being faster in the workers relative to queens. In small, monodomous colonies (Feeding experiment 1), the effect of time was found to be marginally significant ($0.1 > P > 0.05$) however, time was significant when colony population and food abundance were increased to 3,000 workers and 90 queens and 1.05 ml (Feeding experiment 2), respectively (Table 2). Pairwise comparison of feeding experiments 1 and 2 revealed no difference ($P > 0.05$) in the percentage of ants scoring positive for the IgG marker (Table 3). In polydomous colonies with localized food sources (Feeding experiment 3), differences in the percentage of individuals scoring positive for the IgG marker were detected among nest location, caste, and time, and for the nest location by caste and time by caste interactions (Table 3). In the worker caste, food dispersal was significantly greater in nest chamber A 1 h after feeding, with only 12 and 14%, the number of ants scoring positive for the marker in nest chambers B and C, respectively, when compared with nest chamber A. After 8 h, the number of workers exhibiting feeding increased in all three nest chambers, though food dispersal in nest chamber C was still significantly less than in nest chamber A (Table 1). Only queens in nest chamber A exhibited feeding in this trial, though substantially lower when compared with workers. Controlling for nest and time, there was a 9.8-fold increase in food dispersal among workers when compared with queens. In polydomous colonies with dispersed food sources (Feeding experiment 4), differences in the number of ants scoring positive for the IgG marker were detected between castes and for the time by nest location and time by nest location by caste interactions (Table 2). The percentage of workers and queens scoring positive for the IgG marker when controlling for nest location and time were 85 and 62%, respectively, with uniform levels of food dispersal across each nest chamber. Pairwise comparison of feeding experiments 3 and 4 revealed differences in food dispersal between experiments, and for the experiment by nest location, experiment by time by nest location, and experiment by time by nest location by caste interactions (Table 3). The overall number of ants scoring positive for the IgG marker was 3.1-fold greater when all foraging arenas were provided with spiked sucrose

Table 3. Statistical pairwise comparisons of laboratory feeding experiments

Experiment pairwise comparison		Fixed effect	*F*	df	*P* > *F*
Feeding experiment 1: Monodomous, small	**Feeding experiment 2:** Monodomous, large	Experiment	0.01	1,4	0.9223
		Experiment*caste	1.00	1,8	0.3472
		Experiment*time	0.01	1,16	0.9104
		Experiment*time*caste	0.98	1,16	0.3365
Feeding experiment 3: Polydomous, localized food source	**Feeding experiment 4:** Polydomous, dispersed food source	Experiment	73.59	1,4	0.0010
		Experiment*nest location	3.73	2,16	0.0467
		Experiment*caste	2.46	1,24	0.1296
		Experiment*nest location*caste	2.11	2,24	0.1437
		Experiment*time	1.81	1,48	0.1849
		Experiment*time*nest location	4.07	2,48	0.0233
		Experiment*time*caste	0.36	1,48	0.5511
		Experiment*time*nest location*caste	3.21	2,48	0.0493
Feeding experiment 3: Polydomous, localized food source	**Feeding experiment 5:** Polydomous, delayed foraging	Experiment	0.62	1,4	0.4752
		Experiment*nest location	0.83	2,16	0.4521
		Experiment*caste	14.91	1,24	0.0007
		Experiment*nest location*caste	2.57	2,24	0.0976
		Experiment*time	2.48	1,48	0.1221
		Experiment*time*nest location	1.92	2,48	0.1574
		Experiment*time*caste	0.28	1,48	0.6023
		Experiment*time*nest location*caste	0.71	2,48	0.4963

Table 4. Mean ± SE percentage of *T. sessile* samples scoring positive for the IgG marker, grouped by field feeding experiments

Feeding experiment	Nest	Mean percent positive ± SE		
		2 h	8 h	24 h
1: Localized food source	1	57 ± 12 a	10 ± 3 b	5 ± 3 b
	2	22 ± 10 ab	8 ± 8 b	5 ± 3 b
	3	27 ± 12 ab	22 ± 12 ab	2 ± 2 b
	4	12 ± 2 b	12 ± 4 b	2 ± 2 b
2: Dispersed food source	1	35 ± 6 abcd	28 ± 16 abcd	10 ± 6 d
	2	65 ± 10 abc	50 ± 10 abcd	15 ± 13 d
	3	70 ± 15 ab	48 ± 23 abcd	17 ± 12 cd
	4	72 ± 12 a	50 ± 15 abcd	20 ± 8 bcd
3: Donor food sharing	1	57 ± 9 a	33 ± 4 a	32 ± 17 a
	2	25 ± 3 a	10 ± 10 a	13 ± 11 a
	3	37 ± 25 a	5 ± 3 a	2 ± 2 a
	4	32 ± 29 a	5 ± 5 a	3 ± 3 a

Means are separated by nest location and time. Means within experiments that are followed by the same letter are not significantly different using Tukey's HSD test ($P < 0.05$).

Table 5. Statistical comparisons of food dispersal in field colonies of *T. sessile*, measured by nest location and time

Feeding experiment	Fixed effect	*F*	df	*P* > *F*
1: Localized food source	Nest location	2.61	3,6	0.1466
	Time	12.96	2,16	0.0005
	Time*nest location	2.63	6,16	0.0564
2: Dispersed food source	Nest location	1.87	3,6	0.2358
	Time	44.20	2,16	<0.0001
	Time*nest location	1.00	6,16	0.4567
3: Donor food sharing	Nest location	2.22	3,6	0.1861
	Time	5.34	2,16	0.0167
	Time*nest location	0.17	6,16	0.9813

water. Though an increase in food dispersal was evident in both castes when spiked sucrose water was presented into each foraging arena, the rate of increase did not differ between castes. In colonies where food was restricted to foraging arena A for the duration of the feeding period (Feeding experiment 5), differences in the percentage of ants scoring positive for the IgG marker were detected among nest location and caste, and for the time by nest location and time by caste interactions (Table 2). The overall percentage of workers exhibiting feeding was 2.1-fold greater when compared with queens. After 8 h, differences in food dispersal were not present across nests in both castes, and the marker was not detected among queens in either nest chamber B or C. A pairwise comparison between feeding experiments 3 and 5 revealed a difference in the percentage of ants scoring positive for the IgG marker in the experiment by caste interaction (Table 3). For workers, delaying foraging decreased overall food dispersal by 36%. In contrast, a delay in foraging increased food dispersal in queens by 67%.

Field Feeding Experiments. In all field trials, differences in the percentage of ants scoring positive for the IgG marker were detected across time intervals, however ants exhibiting feeding steadily decreased over time (Tables 4 and 5). In colonies with localized food sources (Feeding trial 1), food dispersal at nest 4 was 79% lower relative to nest 1 after 2 h, though the interaction of time by nest was only marginally significant ($0.1 > P > 0.05$). By 24 h, the mean percentage of ants scoring positive for the IgG marker across all nests was only 3%. When spiked sucrose water was placed at every nest in the colony (Feeding trial 2), food dispersal was uniform over the entire colony. The percentage of ants scoring positive across all nests decreased from 60% 2 h after feeding to 44% at 8 h, and 15% at 24 h after feeding. Placing replete workers into nest 1 (Feeding experiment 3) yielded similar results when compared with feeding experiment 1. Statistical differences in the percentage of ants scoring positive for the IgG were not detected between nests after 2 h (Table 4). After 8 h, the percentage of ants exhibiting feeding over the entire colony decreased by 66%, however remained the same after 24 h. Statistical comparison of all feeding experiments revealed differences in the percentage of ants scoring positive for the marker across time ($F = 36.39$; df = 2,48; $P < 0.0001$), and for the of experiment by nest location ($F = 2.92$; df = 6,18; $P = 0.0363$) and experiment by time ($F = 2.76$; df = 4,48; $P = 0.0379$) interactions. Feeding experiment 2 yielded a numerically greater level of food dispersal, with a 2.6- and 1.9-fold greater percentage of ants scoring positive for the IgG marker when compared with feeding experiments 1 and 3, respectively.

Discussion

Results from this study provide evidence that colony structure and resource abundance have an effect on food dispersal in *T. sessile*. In laboratory feeding experiments, colonies consisting of simple, centralized configurations distributed food rapidly throughout the worker caste. Because the food was in close proximity to monodomous colonies, the

time required for foraging was reduced, thus allowing for rapid food exchange. Monodomous colonies generally adhere to smaller spatial boundaries, with a majority of the population confined to specific areas. However, the efficacy of resource collection in monodomous colonies can decrease drastically when food is not in close proximity, primarily due to greater time spent foraging (Debout et al. 2007). Results from large, monodomous colonies revealed that food dispersal rates remained high when the nests were consolidated into a single-nest colony. A high proportion of both workers and queens tested positive after only 1 h, partially due to a substantially smaller foraging space. This suggests that the location of food in relationship to the colony has an effect on the rate of food dispersal. The experimental setup for polydomous colonies simulated an urban colony where nests are typically organized in a linear pattern and connected by trails. With food in close proximity to each nest, colonies uniformly distributed food throughout the entire worker caste. These results are similar to those observed by Buczkowski and Bennett (2006), where the majority of workers within the nest closest to the food source displayed evidence of feeding after 3 h. Other pest ant species, such as *L. humile*, commonly utilize multiple nests to forage effectively in areas that contain ephemeral and dispersed food resources (Heller et al. 2008). A higher rate of resource collection and distribution can also be attributed to an increased level of recruitment across a polydomous colony's expansive territory (Holldobler and Lumsden 1980, Human and Gordon 1996, Holway and Case 2001). It is possible that polydomous colonies with localized resources are less likely to disperse food across the colony as quickly and efficiently, due to social and physical constraints, such as recruitment and trail crowdedness. Lengthier trails, require more time to cross, thus increasing foraging time and decreasing the percentage of individuals that are exposed to the food source per unit time, as examined in polydomous colonies with centralized food sources. Dispersal of food was not as extensive when foraging was delayed in polydomous colonies. Following reinsertion of the bridges, workers from nest A subsequently moved to nests B and C, initiating successive trophallactic exchange. Interestingly, queens in nests B and C showed no evidence of food acquisition, which could imply a delayed feeding behavior. The delay could result from a low queen to worker ratio (1:100), or from a reproductive hierarchy, as observed in other ant species such as *L. humile* (Fournier and Keller 2001).

Field experiments examined food distribution among nests in three distinct polydomous colonies. Results revealed a steady drop in the percentage of ants scoring positive over time in all experiments. This decrease can most likely be attributed to dilution of the protein marker. Though the marker can be detected in trace amounts with the ELISA technique, prolonged trophallactic behaviors may have diluted the marker to a level which failed to exceed the positive threshold, as previously noted with *T. sessile* (Buczkowski and Bennett 2006). One shortcoming of using field colonies is that estimations of population sizes are virtually impossible. Nests were confined to the inside of concrete walls, exposing only interconnecting foraging trails. It is possible, however, that the dilution of the marker implies a high rate of feeding across all nests, coupled with visual evidence of the presence of workers at the feeding stations. When food was centralized, a steady decrease in the percentage of workers scoring positive for the marker was revealed as distance away from the food source increased. This suggests that ants distal from the food source must either travel long distances to feed directly or wait to acquire the food from workers that have traveled the distance and brought the food back to the nest. Higher rates of food distribution (~35–72% after 2 h) were detected when all nests in the colony were provided with food. The nominally higher percentage of positive workers in the mark release recapture experiment can be attributed to the elimination of any foraging. Donors, originating from nest entrance 1, moved across the colony and exchanged food with other nests. Further studies on the use of CMR techniques coupled with immunomarking could provide more accurate results for examining food dispersal patterns in ants.

This study provides further insight into foraging and feeding behaviors in *T. sessile*. Experimental trials demonstrated that food dispersal within both worker and reproductive castes is greater when food is located in close proximity to the nest. In addition, a delayed feeding response appears to be present in the queen caste. Future studies will need to focus on delayed feeding response in order to better assess feeding behaviors in the reproductive caste. This knowledge can be employed for use in improving urban pest management practices, as the presence of *T. sessile* is common in homes and buildings (Smith 1928). Baiting at multiple locations within the colony should increase the proportion of worker, but more importantly, queens, ingesting the bait. The polygynous and polydomous nature of this species in urban environments requires the use of specialized tactics when eliminating colonies, as budding or reestablishment of nests can occur as a result of poor treatment practice (Barbini and Fell 2001). Thus, comprehensive knowledge of feeding behaviors should allow for increased efficacy in integrated pest management programs.

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References Cited

Barbini, L., and R. Fell. 2001. Entomology fact sheet: Odorous house ant. Virginia Cooperative Extension.

Bhatkar, A., and W. H. Whitcomb. 1970. Artificial diet for rearing various species of ants. Fla. Entomol. 53: 229–232.

Boulay, R., A. Hefetz, V. Soroker, and A. Lenoir. 2000. *Camponotus fellah* colony integration: worker individuality necessitates frequent hydrocarbon exchanges. Anim. Behav. 59: 1127–1133.

Buczkowski, G. 2010. Extreme life history plasticity and the evolution of invasive characteristics in a native ant. Biol. Invasions 12: 3343–3349.

Buczkowski, G., and G. W. Bennett. 2006. Dispersed central-place foraging in the polydomous odorous house ant, *Tapinoma sessile* as revealed by a protein marker. Insect. Soc. 53: 282–290.

Buczkowski, G., and G. W. Bennett. 2008. Seasonal polydomy in a polygynous supercolony of the odorous house ant, *Tapinoma sessile*. Ecol. Entomol. 33: 780–788.

Buczkowski, G., and G. W. Bennett. 2009. The influence of forager number and colony size on food distribution in the odorous house ant, *Tapinoma sessile*. Insect. Soc. 56:185–192.

Buczkowski, G., and M. VanWeelden. 2010. Foraging arena size and structural complexity affect the dynamics of food distribution in ant colonies. Environ. Entomol. 39:1936–1942.

Choe, J. C., and D. J. Crespi. 1997. The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge, UK.

Debout, G., B. Schatz, M. Elias, and D. McKey. 2007. Polydomy in ants: what we know, what we think we know, and what remains to be done. Biol. J. Linn. Soc. 90: 319–348.

Fisher, B. L., and S. P. Cover. 2007. Ants of North America: a guide to the genera. University of California Press, Berkeley, CA.

Fournier, D., and L. Keller. 2001. Partitioning of reproduction among queens in the Argentine ant, *Linepithema humile*. Anim. Behav. 62: 1039–1045.

Hagler, J. R. 1997. Protein marking insects for mark-release-recapture method. Trends Entomol. 1: 105–115.

Hagler, J. R., and C. G. Jackson. 1998. An immunomarking technique for labeling minute parasitoids. Environ. Entomol. 27: 1010–1016.

Hagler, J., A. Cohen, D. Bradley-Dunlop, and F. Enriquez. 1992. Field evaluation of predation on *Lygus hesperus* (Hemiptera: Miridae) using a species- and stage-specific monoclonal antibody. Environ. Entomol. 21: 896–900.

Heller, N. E., K. K. Ingram, and D. M. Gordon. 2008. Nest connectivity and colony structure in unicolonial Argentine ants. Insect. Soc. 55: 397–403.

Hölldobler, B., and C. J. Lumsden. 1980. Territorial strategies in ants. Science 210: 732–739.

Hölldobler B., and E. O. Wilson. 1977. The number of queens: an important trait in ant evolution. Naturwissenschaften 64: 8–15.

Holway, D. A., and T. J. Case. 2000. Mechanisms of dispersed central-place foraging in polydomous colonies of Argentine ant. Anim. Behav. 59: 433–441.

Holway, D. A., and T. J. Case. 2001. Effects of colony-level variation on competitive ability in the invasive Argentine ant. Anim. Behav. 61: 1181–1192.

Human, K. G., and D. M. Gordon. 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. Oecologia 105: 405–412.

Markin, G. P. 1970a. Food distribution within laboratory colonies of the Argentine ant, *Iridomyrmex humilis* (Mayr). Insect. Soc. 17: 127–158.

Markin, G. P. 1970b. The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae) in southern California. Ann. Entomol. Soc. Am. 635: 1238–1242.

McIver, J. 1991. Dispersed central-place foraging in Australian meat ants. Insect. Soc. 38: 129–137.

Menke, S. B., W. Booth, R. R. Dunn, C. Schal, E. L., Vargo, and J. Silverman. 2010. Is it easy to be urban? Converegent success in urban habitats among lineages of a widespread ant. PLoS One 5: e9194.

Newell, W., and T. C. Barber. 1913. The Argentine ant. USDA Bulletin 122: 1–98.

Rosengren, R., and P. Pamilo. 1983. The evolution of polygyny and polydomy in mound-building *Formica* ants. Acta Entomol. Fenn. 42: 65–77.

SAS Institute. 2008. SAS/STAT guide for personal computers, version 9.2. SAS Institute, Cary, NC.

Smith, M. R. 1928. The biology of *Tapinoma sessile* Say, an important house-infesting ant. Ann. Entomol. Soc. Am. 21: 307–330.

Traniello, J.F.A. 1989. Foraging strategies of ants. Annu. Rev. Entomol. 34: 191–210.

Wilson, E. O. 1971. Social insects. Science 172: 406.

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