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RESEARCH ARTICLE

The influence of forager number and colony size on food distribution in the odorous house ant, *Tapinoma sessile*

G. Buczkowski · G. Bennett

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Abstract Stomodeal trophallaxis plays a major role in ant colony nutrition and communication. While the rate of food distribution at the individual level (worker to worker) is rapid, factors affecting the rate of food distribution at the colony level remain poorly understood. We used the odorous house ant, *Tapinoma sessile* (Say), as a model species to investigate the factors affecting the rate of spread of liquid carbohydrate food throughout a colony. To track the movement of the food we used protein marking and double antibody sandwich enzyme-linked immunosorbent assay, DAS-ELISA. Increasing colony size while keeping the number of donor workers constant significantly decreased the number of individuals testing positive for the marker. After 8 h of trophallactic interactions with ten donors, 92 ± 5% of recipient workers tested positive in a colony of 125 and 38 ± 5% tested positive in a colony of 1,000. Interestingly, as colony size increased and the percentage of workers testing positive decreased, the proportion of workers actually receiving food increased. Food originating from a single donor fed approximately 12 individuals in colonies comprised of 125 recipients and approximately 38 individuals in colonies comprised of 1,000 recipients. Thus, the per capita consumption of food decreased as colony size increased, most likely because the amount of food reaching the colony was limited. Increasing the number of donors while keeping colony size constant significantly increased the number of recipient ants testing positive for the marker. As the number of donor workers doubled, the percentage of recipients testing positive more than doubled suggesting that the number of individuals receiving food increases with increasing colony size, while the per capita amount of food decreases. When food was available ad libitum and in close proximity to the nest, numerous workers fed directly at the food source. This dramatically increased the rate and the extent of food distribution to both the workers and the queens and colony size had no significant effect on the spread of the marker in the workers or the queens. The rate and the extent of food distribution at the colony level may depend on a number of factors including the number of successful foragers, the size and density of the recipient colony, and the recipient caste.

Keywords Foraging · Immunomarking · Odorous house ant · Protein marking · *Tapinoma sessile* · Trophallaxis

G. Buczkowski (✉) · G. Bennett
Department of Entomology, Purdue University, West Lafayette, IN 47907, USA
e-mail: gbuczkow@purdue.edu

Introduction

Trophallaxis, defined as the regurgitation of food by one animal for another, is a hallmark of highly social insects such as Hymenoptera and Isoptera and is thought to have played a key role in the evolution of sociality (Choe and Crespi, 1997). In eusocial insects, trophallaxis is an important and highly efficient method for delivering food to the various castes and developmental stages that do not or cannot feed directly (Wilson, 1971). Besides this obvious primary function, trophallaxis also plays a crucial role in the exchange of cuticular hydrocarbons among nestmates (Dahbi et al., 1999; Boulay et al., 2000), nutrient cycling (Machida et al., 2001), exchange of information about available food sources (Farina, 1996), as well as transfer of gut symbionts (McMahan, 1969), pheromones (Seeley, 1995) and caste determination hormones (Moore, 1969). In ants, the patterns of social food transfer by

trophallaxis and food allocation from foraging to non-foraging individuals have been thoroughly examined. For example, the rate of exchange of food varies with factors such as season (Khamala and Buschinger, 1971), temperature (Howard and Tschinkel, 1981), and starvation (Markin, 1970; Meudec and Lenoir, 1982). Furthermore, the differential patterns of food allocation based on food type are well documented (Wilson and Eisner, 1957; Sorensen and Vinson, 1981), whereby carbohydrates are mainly used by foragers, lipids by workers and some larvae, and proteins by the growing larvae and egg laying queens.

In ants, the rate and amount of trophallaxis are highly variable, but food is generally transferred within minutes or a few hours and is distributed rapidly throughout the colony (e.g., Markin 1970). A largely liquid diet (e.g., Hemipteran honeydew) and a highly specialized proventriculus are thought to facilitate the rapid transfer of food. Trophallaxis is an open-ended system whereby each worker will share food with one or more nestmates (Wilson and Eisner, 1957). These primary recipients then become secondary donors and each share food with several other nestmates in a process called trophallactic cascade (Suárez and Thorne, 2000). Such pattern of food distribution is hypothesized to be more efficient and result in more equitable distribution than direct transfer which involves transfer only by the original donor.

While the rate of trophallaxis at the individual level (worker to worker) may be rapid, factors affecting the rate of food distribution at the colony level remain poorly understood and relatively little work has been done on the quantitative aspects of trophallaxis with respect to the rate of food distribution. Previous quantitative studies on trophallaxis in ants have focused on species differences in transmission rates (Wilson and Eisner, 1957), the amount of material passed from the foragers to the recipients (e.g., Markin, 1970; Sorensen and Vinson, 1981; Moreira et al., 2006), or effect of colony size and starvation on food distribution (Howard and Tschinkel, 1980).

In principle, there are two ways individual ants can obtain food: they may forage independently and feed directly at the food source or they may rely on foraging individuals and receive food indirectly by trophallaxis. The relative importance of these two mechanisms for the rate and the extent of food distribution within colonies have not been previously estimated. In this study, we used the odorous house ant, *Tapinoma sessile* (Say) as a model species to investigate the factors affecting the rate of spread of liquid carbohydrate food (sucrose solution) throughout a colony. To track the movement of food we used protein marking and double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA; Buczkowski and Bennett, 2006). The goals of this study were twofold. Our main objective was to investigate the effect of forager number (i.e., the donors) and colony size (i.e., the recipients) on the rate and the extent of food distribution. We first examined the effect of increasing the colony size on the rate and the extent of food distribution by introducing a set number of replete foragers into progressively larger colonies. In a second experiment, we examined the effect of increasing the number of replete foragers on the rate and the extent of food distribution by introducing a variable number of foragers into colonies of constant size. These experiments simulate a field scenario where food resources are limited, far away from the nest, and delivered by a limited number of successful foragers. Our second objective was to compare the rate and the extent of food distribution from the first two experiments (i.e., food delivered strictly via foragers and in limited supply) to a situation where the food is more abundant and readily available. We provided colonies with a feeding station that allowed numerous workers ad libitum access to the food. This experiment simulates a field scenario where food is abundant, available locally, and delivered by a relatively large number of foragers. Subsequently, the results of all tests were compared to estimate the relative importance of factors affecting the rate and the extent of food distribution.

Materials and methods

Colonies

Odorous hose ants, *T. sessile* were collected on the campus of Purdue University, West Lafayette, IN from a large polydomous supercolony (Buczkowski and Bennett, 2008). Given the supercolonial nature of *T. sessile* we raised ants collected from numerous nests as a single colony. Debris containing ants was placed in plastic trays provided with moist plaster nests. As the debris dried, the ants moved into plaster nests. Subsequently, colonies were maintained in debris-free, Fluon^{TM}-coated trays. Colonies were reared on 30% sucrose solution and artificial diet (Bhatkar and Whitcomb, 1970) ad libitum and hard-boiled egg and minced crickets once a week. Colonies were maintained and all experiments were conducted at 25 ± 2°C, 60 ± 10% RH, and 14:10 L:D cycle.

Effect of increasing colony size and forager number on food distribution

The rate and the extent of food distribution were examined by introducing a set number of replete donor workers into colonies of varying size. Colony fragments consisting of 125, 250, 500, or 1,000 workers and 20 queens were placed inside 52 × 38 × 5 cm high-Fluon-coated plastic boxes

and allowed to colonize a moist plaster nest (8 cm Ø). The ants were provided with drinking water and allowed to acclimate to the nest for 48 h without food. Following the acclimation period, a group of ten replete donors was introduced into the recipient colonies. To prepare the donors, a group of approximately 200 workers was starved for 24 h and subsequently allowed to feed on a droplet of 30% sucrose solution containing technical grade rabbit immunoglobin (IgG) protein (Sigma Chemical Co., St. Louis, MO, USA) at a concentration of 0.5 mg IgG/mL sucrose. This concentration was selected based on the results of previous studies that revealed that the increases in optical density were minimal above 0.5 mg/mL (Buczkowski and Bennett, 2006). Ants that fed to repletion were gently lifted out of the feeding box using a toothpick and immediately transferred to the recipient colony. To estimate the amount of protein marker acquired by the recipient workers and queens we randomly sampled 10% of the workers (i.e., 12, 25, 50, or 100 individuals) and five queens from each recipient colony at 30, 60, and 480 min after introducing the donors. The number of workers sampled at each time point was equal to 10% of the original colony size, not the number of workers remaining after prior sampling events. All individuals were frozen in individual tubes at −20°C and later analyzed by DAS-ELISA (see below). Three replicates were performed for each colony size using independent colony fragments. In addition, the rate and the extent of food distribution were examined by introducing a variable number of replete donor workers into colonies of constant size. We hypothesized that increasing the number of replete donors while keeping colony size constant would increase the rate of food transmission and result in more thorough distribution due to more food entering the colony. 5, 10, or 20 replete donors were introduced into a recipient colony of 250 workers and 20 queens, prepared as described above. To estimate the amount of protein marker acquired by the recipient workers and queens we randomly sampled 10% of the workers (i.e., 25 individuals) and five queens from each recipient colony at 30, 60, and 480 min after introducing the donors. All individuals were frozen in individual tubes at −20°C and later analyzed by DAS-ELISA. Three replicates were performed for each colony size.

Effect of direct feeding on food distribution

The rate and the extent of food distribution were examined in colonies provided with a feeding station that allowed numerous workers ad libitum access to the food. This experiment simulates a field scenario where food is abundant and available locally (e.g., aggregations of honeydew-producing Hemiptera) and harvested by a relatively large number of workers. Colony fragments consisting of 125, 250, 500, or 1,000 workers and 20 queens were placed inside test boxes and acclimated as above. Following acclimation, colonies were provided with a 1 mL of 30% sucrose solution containing technical grade rabbit immunoglobin (IgG) protein at a concentration of 0.5 mg IgG/mL sucrose. The food was placed approximately 5 cm away from the nest and was available ad libitum for 10 min. Subsequently, the IgG-labeled food was removed and no other food was provided for the remainder of the test. To estimate the amount of protein marker acquired by the workers and the queens we randomly sampled 10% of the workers and five queens from each recipient colony at 30, 60, and 480 min after removing the food. All individuals were frozen in individual tubes at −20°C and later analyzed by DAS-ELISA. Three replicates were performed for each colony size.

ELISA procedure

Sandwich ELISA was performed on individual ant samples using previously described techniques (Buczkowski and Bennett, 2006, 2007). Frozen samples were individually homogenized in 150 μL phosphate buffered saline and assayed for the presence of the rabbit immunoglobin protein. Each well of a 96-well microplate was coated with 100 μL of anti-rabbit IgG (developed in goat) (Sigma Chemical Co., St. Louis, MO, USA) diluted 1:500 in distilled water and incubated for 2 h at 4°C. After incubation, the primary antibody was discarded and 310 μL of 1% non-fat dry milk (Bio-Rad Laboratories, Hercules, CA, USA) in distilled water was added to each well to block any remaining non-specific binding sites. After 30 min incubation at 26°C the milk was discarded. Ant samples were vortexed, added to the wells, and incubated for 1 h at 26°C. The samples were then discarded and each well was washed three times with PBS Tween 20 (0.05%) and two times with PBS. Anti-rabbit IgG conjugated to horseradish peroxidase (50 μL) diluted 1:1,000 in 1% non-fat milk was added to each well and incubated at 26°C for 1 h. All wells were washed again as above and 50 μL of TMB HRP substrate (BioFX Laboratories, Owings Mills, MD, USA) was added to each well and incubated for 30 min. Samples were analyzed on a Beckman Coulter AD 340 Absorbance Detector set at 620 nm. The mean (±SE) optical density value and the percentage of samples scoring positive for rabbit protein were determined. Six negative controls (ants never exposed to rabbit IgG) and six blanks (PBS buffer only) were run on each plate.

Statistical analysis

The samples were scored positive for the presence of the protein marker if the ELISA optical density value exceeded

the mean negative control value by three standard deviations (Sutula et al., 1986; Buczkowski and Bennett, 2006). The percentage of samples testing positive for the IgG protein was tabulated by first calculating the percent of individuals testing positive within a replicate and then averaging across the three replicates. ANOVA tests were conducted to determine the significance of colony size, caste, time, and food delivery method on the spread of the marker. This was accomplished by using the PROC ANOVA (repeated measures ANOVA) procedure in SAS 8.1 (SAS, 2002), followed by post hoc Tukey's HSD tests to separate the means. For all experiments the results are expressed as both: (1) the mean number of individuals testing positive, and (2) the mean optical density (OD).

Results

Effect of increasing colony size and forager number on food distribution

Increasing colony size while keeping the number of donors constant significantly decreased the number of ants testing positive for the marker (Table 1). Colony size had a significant effect on the spread of the marker in the workers ($df = 3$, $F = 9.10$, $P = 0.012$) with $92 \pm 5\%$ of the workers testing positive in a colony of 125 and $38 \pm 5\%$ testing positive in a colony of 1,000 after 8 h of trophallactic interactions with 10 donors. Interestingly, as colony size increased and the percentage of workers testing positive decreased (Fig. 1a), the number of workers actually receiving food increased (Fig. 1b). Eight hours after introducing the donors, 92% of the workers tested positive in a colony of 125 (115 workers), 61% in a colony of 250 (153 workers), 53% in a colony of 500 (265 workers), and 38% in a colony of 1,000 (380 workers). This suggests that food originating from a single donor fed approximately 12 individuals in colonies comprised of 125 recipients and approximately 38 individuals in colonies comprised of 1,000 recipients.

In contrast to the workers, colony size had no significant effect on the spread of the marker in the queens ($df = 3$, $F = 1.00$, $P = 0.455$). This is largely due to delayed distribution of food to the queens and most or all queens initially testing negative for the marker regardless of colony size. In comparison to the workers, a substantially smaller percentage of the queens received sucrose. At 8 h, only $20 \pm 12\%$ of the queens tested positive, while $92 \pm 5\%$ of the workers tested positive. Overall, time had a significant effect on the spread of the marker in the workers ($df = 2$, $F = 25.80$, $P = 0.001$) and the queens ($df = 2$, $F = 10.61$, $P = 0.011$). Generally, the percentage of workers or queens testing positive was not significantly

Table 1 Mean percentage ± SE of recipients testing positive for rabbit IgG protein 30, 60, and 480 min after introducing ten sucrose-fed donors

Donor: recipient ratio	Mean % positive samples					
	Workers			Queens		
	30 min	60 min	480 min	30 min	60 min	480 min
10:125	33 ± 8 b,a (0.31 ± 0.07)	39 ± 6 b,a (0.34 ± 0.08)	92 ± 5 a,a (0.42 ± 0.05)	0 ± 0 a,a (0.05 ± 0.00)	7 ± 7 a,a (0.06 ± 0.01)	20 ± 12 a,ab (0.09 ± 0.02)
10:250	29 ± 5 b,a (0.21 ± 0.04)	35 ± 7 b,a (0.28 ± 0.04)	61 ± 5 a,b (0.33 ± 0.04)	0 ± 0 a,a (0.05 ± 0.00)	7 ± 7 a,a (0.06 ± 0.01)	20 ± 12 a,ab (0.09 ± 0.03)
10:500	9 ± 2 b,b (0.09 ± 0.02)	14 ± 2 b,b (0.09 ± 0.02)	53 ± 6 a,bc (0.20 ± 0.02)	0 ± 0 b,a (0.05 ± 0.00)	0 ± 0 b,a (0.05 ± 0.00)	33 ± 7 a,a (0.11 ± 0.03)
10:1,000	13 ± 2 b,b (0.09 ± 0.01)	18 ± 3 b,b (0.10 ± 0.01)	38 ± 5 a,c (0.16 ± 0.01)	0 ± 0 a,a (0.05 ± 0.00)	0 ± 0 a,a (0.05 ± 0.00)	7 ± 7 a,b (0.06 ± 0.01)

Mean optical density (OD) values ± SE are given in parentheses. Means followed by the same letter within each caste are not significantly different by Tukey's HSD test ($P \leq 0.05$). First letter indicates within row comparisons, second within column comparisons

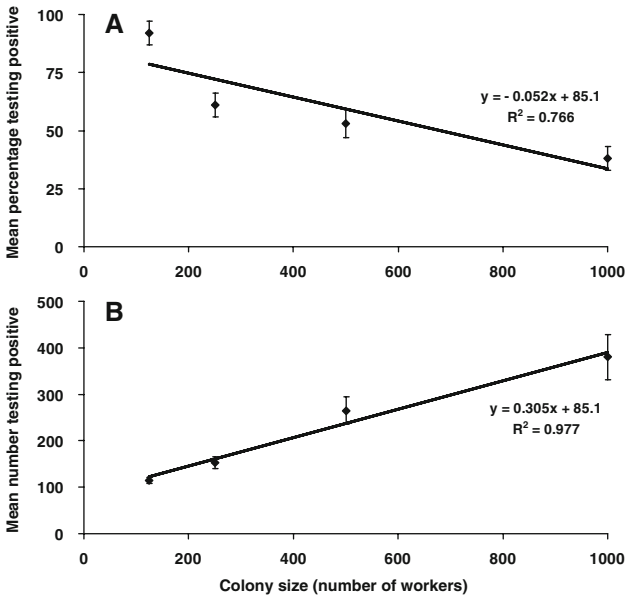

Fig. 1 **a** Mean (±SEM) percentage of *T. sessile* testing positive for the protein marker 8 h after introducing ten donors into colonies of increasing size, **b** the actual number (mean ± SEM) of *T. sessile* workers testing positive for the marker 8 h after introducing the donors

different at 30 and 60 min, but was different at 60 and 480 min (Table 1).

Increasing the number of donors while keeping colony size constant significantly increased the number of recipient ants testing positive for the marker (Table 2). The number of donors had a significant effect on the spread of the marker in the workers ($df = 2$, $F = 45.71$, $P = 0.002$), but not the queens ($df = 2$, $F = 1.00$, $P = 0.444$). At 30 min, 9 ± 5% of the workers tested positive in colonies provisioned with 5 donors, 27 ± 4% in colonies provisioned with 10 donors, and 61 ± 6% in colonies provisioned with 20 donors. As the number of donor workers doubled, the percentage of workers testing positive more than doubled, suggesting that the number of individuals receiving food increases with increasing colony size, but the amount of food an individual receives decreases with increasing colony size. Time also had a significant effect on the spread of the marker in the workers ($df = 2$, $F = 12.54$, $P = 0.019$) and the queens ($df = 2$, $F = 30.25$, $P = 0.004$). Generally, the percentage of workers or queens testing positive was not significantly different at 30 and 60 min, but was different at 60 and 480 min (Table 2).

Effect of direct feeding on food distribution

When food was available ad libitum and in close proximity to the nest, numerous workers fed directly at the food source. This dramatically increased the rate and the extent

Table 2 Mean percentage ± SE of recipients testing positive for rabbit IgG protein 30, 60, and 480 min after introduction of sucrose-fed donors

Donor: recipient ratio	Mean % positive samples					
	Workers			Queens		
	30 min	60 min	480 min	30 min	60 min	480 min
5:250	9 ± 5 b,c (0.06 ± 0.01)	9 ± 1 b,c (0.07 ± 0.01)	44 ± 6 a,b (0.18 ± 0.02)	0 ± 0 a,a (0.05 ± 0.00)	0 ± 0 a,a (0.05 ± 0.00)	13 ± 13 a,a (0.07 ± 0.01)
10:250	27 ± 4 b,b (0.13 ± 0.02)	28 ± 2 b,b (0.14 ± 0.02)	47 ± 6 a,b (0.21 ± 0.03)	0 ± 0 a,a (0.05 ± 0.00)	0 ± 0 a,a (0.05 ± 0.00)	7 ± 7 a,a (0.06 ± 0.01)
20:250	61 ± 6 b,a (0.31 ± 0.04)	64 ± 6 b,a (0.30 ± 0.03)	85 ± 5 a,a (0.35 ± 0.03)	0 ± 0 a,a (0.05 ± 0.00)	0 ± 0 a,a (0.05 ± 0.00)	13 ± 7 a,a (0.06 ± 0.01)

Mean optical density (OD) values ± SE are given in parentheses. Means followed by the same letter within each caste are not significantly different by Tukey's HSD test ($P \leq 0.05$). First letter indicates within row comparisons, second within column comparisons

of food distribution to both the workers and the queens (Table 3). Overall, colony size had no significant effect on the spread of the marker in the workers ($df = 3$, $F = 1.57$, $P = 0.291$) or the queens ($df = 3$, $F = 0.79$, $P = 0.541$), although minor differences due to colony size were detected at 30 min (Table 3). At later sampling times, the marker was uniformly present across all colony sizes and had reached almost all workers and approximately two-third of the queens.

Time also had no overall effect on the spread of the marker in the workers ($df = 2$, $F = 4.17$, $P = 0.073$) or the queens ($df = 2$, $F = 1.74$, $P = 0.253$) with minor differences detected at 30 min (Table 3). Generally, however, when food was abundant and available in close proximity, it reached the majority of individuals relatively quickly (i.e., within the first 30 min) and the increase in the percentage of individuals testing positive at later sampling points was not significant.

Discussion

When the number of replete donors was kept constant, increasing colony size significantly decreased the percentage of workers testing positive for the marker. This is expected as increasing the number of workers in the colony will decrease the number of workers that can be fed when food supply is limited. The striking result is that as colony size increased and the percentage of workers testing positive decreased, the number of workers actually receiving food increased. This suggests that the per capita consumption of food decreased as colony size increased, most likely because the amount of food reaching the colony was limited. Food originating from a single donor was distributed to approximately 12 workers in colonies comprised of 125 recipients and approximately 38 workers in colonies comprised of 1,000 recipients. Based on preliminary results (Buczkowski, unpubl. data) a single *T. sessile* worker ingests 0.3 µL of liquid food (30% sucrose solution) when starved for 48 h. This suggests that individual workers received approximately 0.025 µL of food in colonies comprised of 125 recipients and 0.0079 µL in colonies comprised of 1,000 recipients. Thus, as colony size increased eightfold, the per capita amount of food received by the recipient workers decreased approximately threefold. This suggests that workers in larger colonies are more willing and more likely to share food with nestmates than workers in smaller colonies. The factors responsible for this phenomenon are not well understood, but results by Markin (1970) demonstrate that several factors including the type of food, the degree of hunger, the temperature, and the presence of other foods being distributed at the same time affect the distribution of food delivered to the nest by

Table 3 Mean percentage ± SE of individuals testing positive for rabbit IgG protein 30, 60, and 480 min after 10 min of ad labitum feeding on IgG-labeled sucrose

Donor: recipient ratio	Mean % positive samples					
	Workers			Queens		
	30 min	60 min	480 min	30 min	60 min	480 min
10:125	75 ± 5 b,bc (0.87 ± 0.08)	89 ± 7 ab,a (0.84 ± 0.07)	97 ± 3 a,a (1.06 ± 0.05)	73 ± 7 a,a (0.20 ± 0.03)	53 ± 18 a,a (0.14 ± 0.03)	73 ± 7 a,a (0.19 ± 0.03)
10:250	92 ± 4 a,a (1.03 ± 0.04)	89 ± 5 a,a (0.89 ± 0.05)	87 ± 5 a,b (0.84 ± 0.05)	53 ± 13 a,ab (0.17 ± 0.03)	67 ± 7 a,a (0.15 ± 0.03)	53 ± 7 a,a (0.14 ± 0.03)
10:500	85 ± 24 b,ab (0.95 ± 0.03)	95 ± 1 ab,a (1.05 ± 0.03)	99 ± 1 a,a (0.96 ± 0.03)	27 ± 7 b,b (0.10 ± 0.03)	53 ± 7 ab,a (0.14 ± 0.03)	73 ± 7 a,a (0.16 ± 0.02)
10:1,000	64 ± 4 b,c (0.72 ± 0.03)	82 ± 4 a,a (0.95 ± 0.03)	94 ± 2 a,ab (0.94 ± 0.02)	40 ± 23 a,ab (0.14 ± 0.04)	47 ± 7 a,a (0.13 ± 0.03)	67 ± 7 a,a (0.14 ± 0.02)

Mean optical density (OD) values ± SE are given in parentheses. Means followed by the same letter within each caste are not significantly different by Tukey's HSD test ($P \leq 0.05$). First letter indicates within row comparisons, second within column comparisons

replete donors. Furthermore, experiments by Markin (1970) revealed that in starved colonies, a single donor would pass 90% of its food to approximately 100 workers. In fed colonies, a donor would pass only <30% of its food, but the food would reach approximately the same number of workers. This suggests that food distribution is not a simple hunger response, but rather a complex interaction between the nutritional needs of the colony and the need to obtain information pertaining to foraging. While the role of trophallaxis as a communication channel is well understood in other Hymenoptera, especially honeybees (e.g., Farina, 1996; Farina et al., 2007), little is known about the behavioral aspects of trophallaxis in ants. However, it is likely that *T. sessile* distribute food to a large percentage of workers even when food is scarce in order to communicate information about available food sources and to obtain information about the nutritional needs of the colony. Another reason for a greater proportion of workers receiving food with increasing colony size might be related to changing colony density and encounter rates. We placed colony fragments of different sizes in boxes of identical size making the larger colonies more crowded. Workers in larger colonies encountered each other more frequently which may have resulted in more trophallactic interactions. Previous studies show that crowding increases foraging efficiency in leaf-cutting ants (Dussutour et al., 2007) and encounter rate is an important factor regulating task allocation in ants (Gordon and Mehdiabadi, 1999). Our results also suggest that certain factors limit the distribution of food to all individuals, at least when the food is delivered by a limited number of foragers. This is apparent from the results in Table 1, where only 92% of 125 workers tested positive at 8 h. In colonies of 250 workers, 87% or 153 individuals tested positive. This demonstrates that food originating from 10 donors can feed at least 153 recipients and suggests that all individuals could have received food in a colony of 125. It appears, however, that the trophallactic transfer reaches a point at which the workers no longer share food with nestmates, even though the amount of food they possess is suitable for sharing.

Experiments on the trophallactic flow of sucrose from foraging donor workers to the recipients revealed that workers retained the majority of sucrose. The distribution of sucrose to the queens was limited especially when the food was delivered by 10 replete donors. These results are similar to our previous work (Buczkowski and Bennett, 2006) which demonstrated that liquid carbohydrate food is rapidly distributed among *T. sessile* workers and that workers retain the majority of carbohydrates, while the queens receive substantially less. Markin (1970) investigated the distribution of food in another Dolichoderinae ant, the Argentine ant, and obtained similar results which showed that workers were the primary consumers of liquid carbohydrate food. In other ants too, workers utilized the majority of carbohydrates entering the colony (e.g., Wilson and Eisner, 1957; Sorensen et al., 1980). When the food was provided ad libitum for the first 10 min, the amount of sucrose distributed to both the workers and the queens increased significantly, especially at 30 and 60 min after introducing the food. The increase was particularly dramatic in the queens, indicating that carbohydrates are more likely to be delivered to the queens when they are abundant. Furthermore, the effect of colony size and sampling time that was highly significant when the food was delivered by ten replete donors largely disappeared when food was provided ad libitum. This suggests that more workers feed directly when food is provided nearby which increases the number of potential donors and consequently increases the amount of food reaching the colony. We show that increasing the number of donors while keeping colony size constant significantly increases the number of recipient ants testing positive for the marker. Furthermore, when the number of donor workers doubled, the percentage of workers testing positive more than doubled. This suggests that the number of individuals receiving food increases with increasing colony size, while the per capita amount of food decreases.

In addition to providing experimental evidence on the pathways of food distribution in *T. sessile*, the results also provide an insight into the impact of colony-level foraging efficiency on food distribution in *T. sessile*. In ants, foraging efficiency can vary according to numerous factors including food quality (Taylor, 1977), caste and worker size (Traniello, 1987), crowding on the foraging trail (Dussutour et al., 2007), the spatial distribution of nests (Buczkowski and Bennett, 2006; van Wilgenburg and Elgar, 2007), and distance to food (Martin and Vinson, 2008). In our study, experiments utilizing ten replete donors represent low colony-level foraging efficiency where the workers forage for food resources that are intermittent or limited, possibly far away from the nest and thus costly to obtain, and retrieved by a limited number of successful foragers. In contrast, the experiment where numerous workers fed ad libitum represents high colony-level foraging efficiency and simulates a field scenario where food is abundant and available locally (e.g., stable aggregations of honeydew-producing Hemiptera) and consistently harvested by a relatively large number of workers. Our results show that improvements in the colony's foraging strategy, such as finding a stable food resource, can significantly improve the colony's nutritional status and possibly colony productivity. Stable food resources can be more efficiently exploited by reducing travel distances and travel time (McIver, 1991; Davidson, 1997). *T. sessile* frequently utilize Hemipteran aggregations as food (Buczkowski and Bennett, 2008) and their ecological success in invaded

urban areas may largely depend on the availability of Hemipteran honeydew and the ant's ability to utilize such food sources efficiently.

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References

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

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

Buczkowski G. and Bennett G.W. 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 Bennett G.W. 2007. Protein marking reveals predation on termites by the woodland ant, *Aphaenogaster rudis*. *Insect. Soc.* **54**: 219–224

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

Choe J.C. and Crespi D.J. (Eds) 1997. *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge University Press, Cambridge, UK. 541 pp

Dahbi A., Hefetz A., Cerda X. and Lenoir A. 1999. Trophallaxis mediates uniformity of colony odor in *Cataglyphis iberica* ants (Hymenoptera, Formicidae). *J. Insect Behav.* **12**: 559–567

Davidson D.W. 1997. Foraging ecology and community organization in desert seed-eating ants. *Ecology* **58**: 725–737

Dussutour A., Beshers S., Deneubourg J.-L. and Fourcassié V. 2007. Crowding increases foraging efficiency in the leaf-cutting ant *Atta colombica*. *Insect. Soc.* **54**: 158–165

Farina W.M. 1996. Food exchange by foragers in the hive- a means of communication among honey bees? *Behav. Ecol. Sociobiol.* **38**: 59–64

Farina W.M., Grüter C., Acosta L. and Mc Cabe S. 2007. Honeybees learn floral odors while receiving nectar from foragers within the hive. *Naturwissenschaften* **94**: 55–60

Gordon D.M. and Mehdiabadi N.J. 1999. Encounter rate and task allocation in harvester ants. *Behav. Ecol. Sociobiol.* **45**: 370–377

Howard D.F. and Tschinkel W.R. 1980. The effect of colony size and starvation on food flow in the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol*. **7**: 293–300

Howard D.F. and Tschinkel W.R. 1981. The flow of food in colonies of the fire ant, *Solenopsis invicta*: a multifactorial study. *Physiol. Entomol.* **6**: 297–306

Khamala C.P.M. and Buschinger A. 1971. Effect of temperature and season on food-transmission. Activity of three ant species as shown by radioactive tracers. *Z. Angew. Entomol.* **67**: 337–342

Machida M., Kitade O., Miura T. and Matsumoto T. 2001. Nitrogen recycling through proctodeal trophallaxis in the Japanese damp-wood termite *Hodotermopsis japonica* (Isoptera, Termopsidae). *Insect. Soc.* **48**: 52–56

Markin G.P. 1970. The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae) in southern California. *Ann. Entomol. Soc. Am.* **63**: 1238–1242

Martin J.B. and Vinson S.B. 2008. The influence of travel distance on sugar loading decisions and water balance in the central place foraging ant *Solenopsis invicta*. *Insect. Soc.* **55**: 129–136

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

McMahan E.A. 1969. Feeding relationships and radioisotope techniques. In: *Biology of Termites, vol. 1.* (K. Krishna and Weesner F. M., Eds), Academic Press, New York. pp 387–406

Meudec M. and Lenoir A. 1982. Social responses to variation in food supply and nest suitability in ants (*Tapinoma erraticum*). *Anim. Behav.* **30**: 284–292

Moore B.P. 1969. Biochemical studies in termites. In: *Biology of Termites, Vol. 1* (K. Krishna and Weesner F.M., Eds), Academic Press, New York, NY. pp 407–432

Moreira D.D.O., Erthal M. Jr., Carrera M.P., Silva C.P. and Samuels R.I. 2006. Oral trophallaxis in adult leaf-cutting ants *Acromyrmex subterraneus subterraneus* (Hymenoptera: Formicidae). *Insect. Soc.* **53**: 345–348

SAS Institute. 2002. SAS/STAT guide for personal computers, version 8.1. SAS Institute, Cary, NC

Seeley T.D. 1995. *The Wisdom of the Hive*. Harvard University Press, Cambridge, MA 318 pp

Sorensen A.A., Kamas R. and Vinson S.B. 1980. The biological half-life and distribution of 125 iodine and radioiodinated protein in the imported fire ant, *Solenopsis invicta* Buren. *Entomol. Exp. Appl.* **28**: 247–258

Sorensen A.A. and Vinson S.B. 1981. Quantitative food distribution studies within labor colonies of the imported fire ant, *Solenopsis invicta* Buren (1). *Insect. Soc.* **28**: 129–160

Suárez M.E. and Thorne B.L. 2000. Rate, amount, and distribution pattern of alimentary fluid transfer via trophallaxis in three species of termites (Isoptera: Rhinotermitidae, Thermopsidae). *Ann. Entomol. Soc. Am.* **93**: 145–155

Sutula C.L., Gillett J.M., Morrissey S.M. and Ramsdell D.C. 1986. Interpreting ELISA data and establishing the positive-negative threshold. *Plant Disease* **70**: 722–726

Taylor F. 1977. Foraging behavior in ants: experiments with two species of myrmicine ants. *Behav. Ecol. Sociobiol.* **2**: 147–168

Traniello J.F.A. 1987. Comparative foraging ecology of north temperate ants: the role of worker size and cooperative foraging in prey selection. *Insect. Soc.* **34**: 118–130

Van Wilgenburg E. and Elgar M.A. 2007. Colony structure and spatial distribution of food resources in the polydomous meat ant *Iridomyrmex purpureus*. *Insect. Soc.* **54**: 5–10

Wilson E.O. 1971. *The Insect Societies*. The Belknap Press of Harvard University Press, Cambridge, MA. pp 548

Wilson E.O. and Eisner T. 1957. Quantitative studies of liquid food transmission in ants. *Insect. Soc.* **4**: 157–166