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Colony foraging allocation is finely tuned to food distance and sweetness even close to a bee colony

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Abstract

Social bee colonies can allocate their foraging resources over a large spatial scale, but how they allocate foraging on a small scale near the colony is unclear and can have implications for understanding colony decision-making and the pollination services provided. Using a mass-foraging stingless bee, *Scaptotrigona pectoralis* (Dalla Torre) (Hymenoptera: Apidae: Meliponini), we show that colonies will forage near their nests and allocate their foraging labor on a very fine spatial scale at an array of food sources placed close to the colony. We counted the foragers that a colony allocated to each of nine feeders containing 1.0, 1.5, or 2.0 M sucrose solution [31, 43, and 55% sucrose (wt/wt), respectively] at distances of 10, 15, and 20 m from the nest. A significantly greater number of foragers (2.6–5.3 fold greater) visited feeders placed 10 vs. 20 m away from the colony. Foraging allocation also corresponded to food quality. At the 10-m feeders, 4.9-fold more foragers visited 2.0 M as compared to 1.0 M sucrose feeders. Colony forager allocation thus responded to both differences in food distance and quality even when the travel cost was negligible compared to normal colony foraging distances (10 m vs. an estimated 800–1 710 m). For a nearby floral patch, this could result in unequal floral visitation and pollination.

Introduction

Understanding how social bee colonies respond to the quality and spatial distribution of food resources in their environment provides greater insight into colony decision making and has implications for the pollination service that bees provide. Bees, like many other animals, tend to exploit food sources according to their reward value (Pyke, 1984) and can optimize the net rate of energy gain or foraging efficiency (Houston & McNamara, 2014). Two factors, energetic gain (sucrose concentration and volume) and energetic cost (distance or travel time), play major determining roles. For example, honey bees can adjust the rate of forager

arrivals (Fernandez & Farina, 2005), recruitment, and forager abandonment (Seeley et al., 1991) according to food caloric value (sugar concentration) and thereby maximize foraging efficiency (Schmid-Hempel et al., 1985; Kacelnik et al., 1986). Similarly, stingless bees (*Melipona fasciata* Latreille) increase recruitment to a feeder with rising sucrose concentration and decrease recruitment for a feeder with declining sucrose concentration (Biesmeijer & Ermers, 1999).

Travel distance also plays a role. The economics of foraging predicts that distant resources will attract foragers only if they provide rewards that compensate for the costs of energy and time spent in flying greater distances (Cresswell et al., 2000). Given the time and energy costs of travel, foragers should focus on resources closer to their nest (Pyke, 1984), even if the closer resource offers somewhat poorer food. For example, a closer food source (50 m away) offering 0.75 M sucrose solution elicited more honey bee recruitment dances – a measure of colony foraging allocation – than a more distant food source

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(1 000 m) offering richer 1.0 M sucrose (Seeley et al., 1991).

It is therefore somewhat surprising when foragers do not visit rich, nearby resources and prefer to forage farther from the nest. Some observations suggested that honey bees may not forage near their nests, even if good natural forage is available close to the nest (Buchmann & Shipman, 1991). Harmonic radar tracking demonstrated that bumble bees foraged at distances >200 m, although closer natural forage was available (Osborne et al., 2001). Dramstad et al. (2003) showed that bumblebee colonies increasingly used a natural floral resource when the colony was moved further away (>100 m) from the resource.

There are several potential explanations for such long-distance foraging preferences: it may limit predation risk to the colony (Dukas & Edelman-Keshet, 1998), help decrease parasitism (Dramstad, 1996), and reduce visitation of food sources already found and being exploited by colony members (Dramstad, 1996). There are also potential discovery benefits. Flying further may be beneficial if foragers thereby have a higher chance of encountering profitable food (Visscher & Seeley, 1982; Osborne et al., 2001).

In general, studies have focused on relatively long-distance foraging. However, it is unclear whether travel over short distances (<20 m) or time (ca. 4 s for this distance, estimated from Esch & Burns, 1996) will alter a colony's foraging allocation. It makes sense for bees to forage closer to the nest when equally good food is available at different distances. However, models demonstrating this have typically examined far larger ranges: hundreds of meters (Dukas & Edelman-Keshet, 1998; Cresswell et al., 2000). What will bees do when food is extremely close to the nest?

There is a natural context for such close foraging because floral patches can occur close to bee colonies (Buchmann & Shipman, 1991; Dramstad et al., 2003). Moreover, small-scale patch usage may play an important role in the foraging ecology of social bees (Bennett et al., 2014). At very close distances, colonies could simply allocate their foragers uniformly to food of equal quality, regardless of distance. However, our preliminary observations suggested that stingless bee foragers would forage at such close distances and prefer to visit closer feeders.

We therefore tested whether a highly social bee colony can fine tune its foraging over a small spatial scale by measuring how the colony allocates foraging to a nearby patch, ranging from 10 to 20 m away. We manipulated two variables, sucrose concentration and distance, and hypothesized that the colony would allocate foragers according to sugar concentration, but minimally to distance, at such short distances. Differences in foraging allocation to the same sucrose concentrations over these short distances

would demonstrate that the colony can tune its foraging to slight differences in foraging distance and may respond to even small differences in travel costs.

Materials and methods

Study species

We used *Scaptotrigona pectoralis* (Dalla Torre) (Hymenoptera: Apidae: Meliponini), a common stingless bee that ranges from central Panama to Mexico (Roubik, 1992). This species has economic value because it is reared for meliponiculture in Mexico and Costa Rica (Cortopassi-Laurino et al., 2006) and is a crop pollinator of cucurbits (Meléndez-Ramírez et al., 2002) and avocado (Slaa et al., 2006). All stingless bees are highly social (Michener, 2000), and *S. pectoralis* foragers can also rapidly recruit nestmates to good food sources (Slaa et al., 1998; Jarau et al., 2011). Bee foraging ranges correlate with body size and, based upon its body size, *Scaptotrigona postica* (Latreille) may forage up to 1 710 m from the nest (Araujo et al., 2004). The similarly sized *S. pectoralis* may have a comparable flight range, but can also be trained to food sources close to the nest (Reichle et al., 2010), a pre-condition for our study. In addition, *S. pectoralis* collects natural nectar with a broad range of sugar concentrations [22–59% sugar (wt/wt); Roubik et al., 1995], allowing us to test colony response to a wide range of sugar reward values.

Study site and colonies

We sequentially used five colonies of *S. pectoralis* originally obtained from natural colonies in tree-cavities around Tuxtla Gutiérrez, Chiapas, Mexico. We housed each colony in a wood box (25 × 25 × 50 cm) with a circular, 1-cm-diameter entrance. To ensure that foragers came from the focal colony, we placed only one colony at a time at our test site at the Universidad de Ciencias y Artes de Chiapas, in Tuxtla Gutiérrez. The focal colony therefore had no competition when foraging at the feeder array. We used two colonies from September to December 2012 (the beginning of the dry season) and three more colonies from December 2013 to February 2014 (the dry season). During this period, natural floral resources were relatively abundant and colonies were strong, with a large foraging force. We conducted one trial per day, between 09:00 and 15:00 hours. Each trial lasted ca. 2 h, including training time.

Training

The experimental bee colonies had no prior experience with our feeders. They were obtained from natural colonies located at least 50 km away from our field site. The average maximum foraging range of stingless bees is ca.

800 m (van Nieuwstadt & Iraheta, 1996) and *S. pectoralis* forages up to 1 710 m from the nest (Araujo et al., 2004). However, in exceptional circumstances (a dry landscape with very little food), foraging can range up to 2.1 km (Kuhn-Neto et al., 2009). To facilitate rapid training, we used an unscented 2.0 M [55% (wt/wt)] sucrose solution, which is in the upper range of what stingless bee foragers collect from blossoms (Roubik et al., 1995).

Each feeder consisted of a cotton ball soaked in sucrose solution and placed in the center of a 10 × 10 cm square of yellow foam, elevated by a 1-m-high tripod for training and by a 1-m high stake at the final feeder position (method of Sánchez et al., 2008). During training, all feeders provided unscented 2.0 M sucrose solution. We began by injecting 5 ml of unscented 2.0 M sucrose solution into the colony entrance and placing the feeder 2 cm away (method of von Frisch, 1967). Once bees found the feeder, we gradually moved it over 20 min in short steps. At all times during training, we allowed approximately five bees on each feeder. Once more bees visited, we either moved the feeder or set out the next training feeder. In this way, we kept visitation levels and potential odor marking on the feeders fairly constant.

To test for a possible ‘training order’ effect, we trained bees from the near to far feeder (‘start-near’ treatment) or from far to near feeder (‘start-far’ treatment). We began by training bees to the central feeder positions shown in Figure 1, either 10 m (near) or 20 m (far) from the colony. Once bees had been trained to the first feeder, we placed feeders 5 m to its left and right and trained bees to these feeders (Figure 1). After bees were trained to this first row

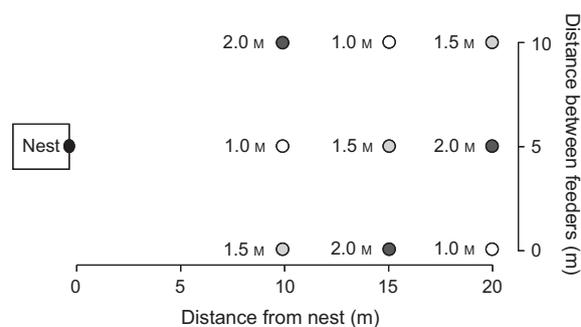


Figure 1 The location and sucrose concentration of feeders relative to the *Scaptotrigona pectoralis* nest. For clarity, the nest box size and the feeder diameters are not shown to scale, but the relative positions of the nest entrance (black oval) and the feeders are to scale. During training, the feeders all had 2.0 M sucrose solution. During the testing phase, these feeders were replaced with new clean feeders with different sucrose concentrations: 1.0 M (white circles), 1.5 M (light gray), or 2.0 M (dark gray).

of feeders, we began training bees to the feeder in the center of the next row (either further away from or closer to the colony, depending upon the treatment) and proceeded until all feeders were set out and approximately five bees visited each feeder. We then began the experiment. Because of the large number of recruits involved in our experiment, we did not mark our bees. Marking all recruits would be difficult and could cause disturbances at feeders with more bees. We therefore used a repeated measures analysis in which each trial was a replicate nested within a colony. We conducted seven replicate trials with colony 1, eight with colony 2, three with colony 3, nine with colony 4, and three with colony 5.

Experiment

After training, we immediately began our experiment, replacing the old feeders to remove odor marks potentially deposited by bees and to provide different concentrations of sucrose. Stingless bees tend to odor mark conspicuous objects elevated above the ground (Nieh et al., 2004). In our case, we observed them only landing and odor marking (as described in Jarau et al., 2011) on the yellow feeder bases that we elevated 1 m above the ground.

To begin the experiment, several assistants simultaneously removed the old odor-marked feeding platforms and replaced them with clean yellow bases with new cotton balls, but now soaked with an equal volume of three unscented sucrose solutions: 1.0, 1.5, and 2.0 M, corresponding to 31, 43, and 55% sucrose (wt/wt), respectively. We chose these sucrose concentrations because *S. pectoralis* collects natural nectars with sugar concentrations ranging from 22 to 59% (wt/wt) (Roubik et al., 1995). We distributed these sucrose concentrations randomly, with each concentration at three feeders (Figure 1). We then waited 1 h for the colony to distribute its foragers among the feeders and counted the bees in the array. The volume of sucrose solution provided was sufficient to last this entire hour and did not need to be refilled. In our trials, we observed that a maximum of ca. 30 bees could forage unrestricted on each feeder (see Figure 2).

Natural inflorescences do not typically provide such abundant nectar, although some rich tropical inflorescences, like lotus flowers, can each support a large number of simultaneous insect foragers (Li & Huang, 2009). However, a very rich natural food patch can be exploited by stingless bees for an even longer period of time, although nectar sugar concentration and quantity will vary over the course of a day (Roubik & Buchmann, 1984). Thus, our feeders simulated very rich patches that were very closely spaced. We choose 1 h as our trial duration because Slaa & van Nieuwstadt (1997) reported that *S. pectoralis* has a sharp increase in recruitment in the first 15 min, followed

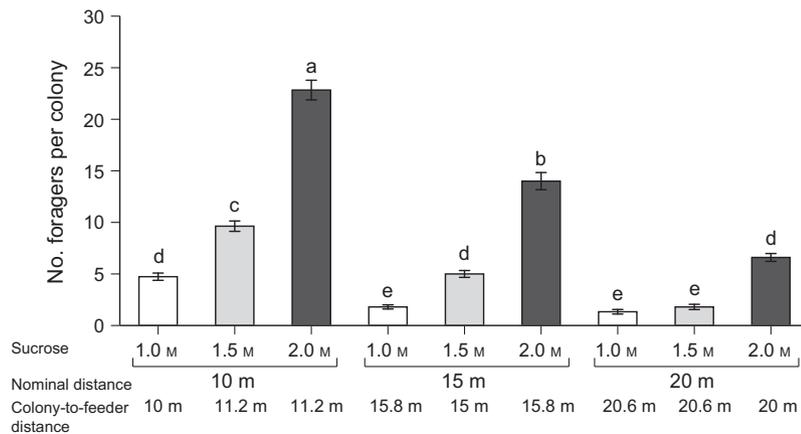


Figure 2 How the colony distributes its foraging force within a food patch offering different sucrose concentrations (1.0–2.0 M) at different nominal distances from the nest (10–20 m; the actual distances are also indicated). Mean (\pm SE; $n = 30$ trials) number of *Scaptotrigona pectoralis* foragers per colony are shown. Means capped with different letters are significantly different (Tukey's HSD tests: $P < 0.05$).

by a lowered rate of recruitment, plateauing at ca. 60 min for a rich food source: [60% sucrose solution (wt/wt)]. Because our feeders did not deplete over the course of 1 h, they provided a situation in which the colony could achieve a stable labor allocation, facilitating our measurements. A food source that depletes more rapidly should show similar trends of distance and sucrose concentration (as predicted by optimal foraging theory), but with lower numbers of bees and perhaps greater variance.

Feeder array distances

Our placement of the feeders in a square array created slight differences in straight-line feeder-to-nest distances (Figure 1). For example, in the 10-m treatment, the center feeder was 10 m from the nest and the two flanking feeders were each 11.2 m from the nest (12% difference; Figure 1). For the 15 m and 20 m treatment locations, these distance differences decreased to 5 and 3%, respectively. Placing the feeders in concentric curves relative to the colony would have resolved this problem, but would also have altered the symmetrical distances among the feeders. We wished to equalize, as much as possible, spacing between feeders as this spacing can affect individual bee foraging choices (Waddington & Holden, 1979).

Statistical analysis

Our analysis treats the colony as an individual whose behavior we repeatedly sample in multiple trials. To address two types of questions, we ran two different analyses. First, we tested for significant differences between the number of foragers that colonies allocated to each feeder distance and sucrose concentration with a univariate repeated-measures ANOVA (REML algorithm), using the log-transformed number of bees on each feeder as the response variable (Lehman et al., 2005). Our fixed effects are training order (start-near or start-far) and treatment (all possible combinations of sucrose and distance, yield-

ing nine treatments). Colony identity is a random effect. We used Tukey's honestly significant difference (HSD) post-hoc tests to make pairwise comparisons between all treatments and thereby extracted the effects of distance and sucrose concentration. For this analysis, analyzing the feeder distances as fixed distances between feeders (Figure 1) or as the feeder-to-nest distances (Figure 2) yields identical results because each feeder is a separate treatment category.

Second, we wished to explicitly test the effects of distance, sucrose concentration, and their interaction (all fixed effects). For this analysis, we used the actual feeder-to-nest distances (see above) because the colony allocates foraging relative to the nest location. To deal with the issue of testing each colony multiple times, we obtained a single value, per colony, for the average number of foragers (log-transformed) at each distance and sucrose concentration. We then used ANOVA (REML algorithm, because colony is a random effect). We report the effect coefficients and tested whether the coefficient significantly differed from 0 with t-tests. We used JMP Pro v11 software for all analyses. All data met parametric assumptions as determined through residuals analysis (Zar, 1984).

Results

Overall treatment effects

In the full repeated-measures model, there is no significant interaction of training order*treatment ($F_{8,248.7} = 1.06$, $P = 0.39$). We therefore used a reduced model without this interaction. The reduced model fits our data ($R^2 = 0.82$). In this model, colony accounts for only 4.6% of variance, and there is no significant effect of training order ($F_{1,2.4} = 3.43$, $P = 0.18$). Thus, training the bees from near-to-far or from far-to-near yields the same distribution of foragers.

However, there is a highly significant effect of treatment ($F_{8,256.7} = 140.4$, $P < 0.0001$). The colony allocated more foragers to closer feeders over all sucrose concentrations (Tukey's HSD tests: $P < 0.05$; Figure 2). The number of foragers was 3.5, 5.3, and 3.6-fold greater at 10 vs. 20 m, for 2.0, 1.5, and 1.0 M sucrose solutions, respectively. There is a strong effect of distance. For the highest concentration sucrose (2.0 M), the number of foragers was greatest at 10 m and decreased at 15 and 20 m, with all pairwise differences significant (Tukey's HSD tests: $P < 0.05$). The same pattern occurred for 1.5 M sucrose. At the lowest concentration (1.0 M), more foragers visited the closest feeder but equal numbers visited the 15 and 20 m locations (Figure 2).

Although all feeders offered relatively good food, the effect of sucrose concentration is strong. At each treatment distance, colonies allocated significantly more foragers to the sweetest feeder and the fewest foragers to the least sweet feeder (Figure 2). For example, at 10 m, colonies allocated 4.9 and 2.0-fold more foragers to 2.0 and 1.5 M sucrose as compared to 1.0 M sucrose. All pairwise comparisons are significant (Tukey's HSD tests: $P < 0.05$), with the exception of the 20 m distance, for which the 1.0 and 1.5 M sucrose solutions attracted equal numbers of foragers.

Detailed distance and sucrose concentration effects

This analysis uses the average number of foragers, per colony, at each distance and sucrose concentration. In the full model ($R^2 = 0.92$) there is a significant effect of distance ($F_{1,37} = 160.04$) and sucrose concentration ($F_{1,37} = 252.71$, both $P < 0.0001$). Colony accounts for 18.5% of model variance. The effect of the distance*sucrose concentration interaction is borderline significant ($F_{1,37} = 4.00$, $P = 0.053$). Specifically, colonies allocated 1.2 fewer foragers for each 10 m of increased distance (parameter estimate = -0.12 , $t = -12.65$, $d.f. = 37$, $P < 0.0001$). Colonies allocated 1.4 more foragers for each 1 M increase in sucrose concentration (parameter estimate = 1.4 , $t = -15.90$, $d.f. = 37$, $P < 0.0001$). The parameter estimate for the interaction distance*concentration is nearly significantly different from 0 (parameter estimate = -0.05 , $t = -2$, $d.f. = 37$, $P = 0.053$).

Discussion

We studied how mass-foraging social bee colonies allocate their foraging force among a patch of nearby food sources with identical appearances but different sucrose reward concentrations at different distances. First, *S. pectoralis* colonies would forage in large numbers quite close to their nests. Second, there is a very clear and strong effect of

distance even though the farthest food source was about 20 m from the colony, a very short distance considering that this species likely forages up to 1 710 m from the nest (Araujo et al., 2004). The colony allocated fewer foragers to feeders further from the nest, even when they offered the same sucrose concentration as feeders only 5 m away, 0.3% of the estimated foraging range.

Why does this occur? It seems unlikely that such very short distances (5 m) impose a travel cost that can account for the large observed shifts in colony labor allocation. The nature of the food source may provide one explanation. We observed a maximum of 33 bees on the richest feeders (offering 2.0 M sucrose). This limited access may have contributed to the colony distributing its foraging force among feeders with lower sucrose concentrations. Bees flying back and forth could therefore have accumulated at the feeders closer to the nest. Attractive odor marks deposited by foragers could also have accumulated at the feeders closer to the nest, driving this trend. However, this simple mechanism does not completely account for our results, because even the closest feeders show a distribution of bees according to sugar concentration.

If our results were due to (1) a higher number of bees more familiar with the older training feeder positions, or (2) bees more attracted to residual odor marks, the start-far and the start-near treatments should have had different distance distributions, with more bees at the feeders to which they were first trained. However, both start-near and start-far treatments resulted in the same distribution of more foragers closer to the nest.

It is not clear whether stingless bees maximize the net rate of gain or energetic efficiency. Honey bees maximize efficiency (Schmid-Hempel et al., 1985; Kacelnik et al., 1986), and bumble bees may maximize efficiency or the net rate of gain (Charlton & Houston, 2010). We predict that stingless bees will maximize the net rate of gain, because they share relevant foraging similarities with honey bees, the only other group of highly social corbiculate bees. Both stingless bees and honey bees typically (1) have large colonies with a high demand for food provisioning (Roubik, 1989), (2) will mass recruit to good food sources by communicating food location (Nieh, 2004), and (3) have foragers of relatively uniform size (Michener, 2000). Forager size is relevant because larger bees have a higher foraging rate than smaller bees (Spaethe & Weidenmuller, 2002).

There are other reasons to suspect that stingless bees may maximize efficiency. Stingless bees are often associated with exploiting dense flower patches (Roubik, 1989), a feature they share with honey bees, which maximize energy efficiency (Essenberg, 2013). Our data do not allow us to test individual forager movement rules or to

determine which currency best accounts for *S. pectoralis* foraging behavior. However, the rapid decrease in the number of foragers with slight increases in distance suggest that they may maximize efficiency, like honey bees. Modeling shows that when bees maximize efficiency, the decrease in bees with distance is much greater than when bees maximize net energy intake (Dukas & Edelstein-Keshet, 1998). This is consistent with our results.

Given the extremely close spacing of the foraging array (ranging from 10 to 20 m from the colony), we expected colonies to distribute their foraging force mainly according to sucrose concentration, not distance. Yet, even in the absence of intercolonial feeder competition, *S. pectoralis* colonies showed strong distance-dependent changes in how they allocated foraging to food of equal quality at very close distances. For the 2.0-M sucrose feeder, a mere 10-m distance increase reduced the average number of foragers by 3.5-fold. This suggests a fine parsing of foraging allocation that has not been previously considered for food sources close to the nest and demonstrates the ability of a colony to allocate its resources, even to slight differences in the spatial distribution of resources. If colonies apply the same rules to a nearby floral patch, this should result in highly unequal floral visitation and could affect pollination.

Future studies could test whether stingless bees maximize the net rate of gain or energetic efficiency by following standard techniques (Houston & McNamara, 2014). It would be particularly interesting to determine whether the currency used changes when bees encounter strong competition at a food resource. Competition from other stingless bees, including dominant aggressive species, may play an important role in the evolution of stingless bee recruitment communication and foraging strategies (Lichtenberg et al., 2010, 2014).

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