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Colony and Individual Forager Responses to Food Quality in the New World Bumble Bee, *Bombus occidentalis*

Henry Nguyen · James C. Nieh

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Abstract The ability of a successful forager to activate colony foraging allows colonies to rapidly exploit ephemeral resources and is an important innovation in the evolution of sociality. We tested the ability of the species, *Bombus occidentalis*, to stimulate colony foraging for food varying in quality. We then analyzed the behavior of successful foragers inside the nest to learn more about potential foraging activation movements. The number of bees entering a foraging arena was positively correlated with food sucrose concentration (0.5, 1.0, and 2.5 M sucrose, equal to 16–65% w/w). Foragers spent significantly more time imbibing higher concentration solutions. Foragers then returned to the nest where they moved in elaborate paths at variable speeds. There was no significant effect of sucrose concentration on average forager velocity or time spent inside the nest. However, the length of a forager's path inside the nest (total of all distances moved each 0.1 s) significantly increased with sucrose concentration. On average, individuals foraging on 2.5 M and 1.0 M solution walked paths respectively 1.6 fold and 1.4 longer than the paths of individuals foraging on 0.5 M solution. These longer paths could result in a greater number of nestmate contacts, a factor shown to be important in the activation of *B. impatiens* foragers and also reported in *B. terrestris* foragers.

Keywords Bumble bee · foraging activation · food alertment · foraging · recruitment · communication · information flow

Introduction

Foraging activation is an increase in colony foraging following the return of a successful forager. Such activation may result from cues such as the food odor brought back by the forager or from signals such as specific excitatory behaviors or

H. Nguyen · J. C. Nieh (✉)
Division of Biological Sciences, Section of Ecology, Behavior, & Evolution, University of California San Diego, Mail code 0116, 9500 Gilman Drive, La Jolla, CA 92093, USA
e-mail: jnieh@ucsd.edu

pheromones (Dornhaus and Chittka 2004). Honey bees and some stingless bee species have been studied as models of foraging activation in which nestmates can communicate resource location (Lindauer and Kerr 1958; von Frisch 1967). Bumble bees are important pollinators in a wide variety of ecosystems (Goulson 2003). However, relatively little is known about how they activate colony foraging, especially in comparison to the honey bees (Kitaoka and Nieh 2009). Unlike honey bees, bumble bee foragers can activate nestmates to search for food of the same scent, but do not appear to communicate its location (Dornhaus and Chittka 1999, 2004). This strategy is interesting because it may represent an ancestral state in the evolution of bee recruitment communication (Dornhaus and Chittka 2001). The closest ancestor of bumble bees (Bombini) is not topologically basal to the closest ancestors of the highly social bees (Apini and Meliponini, Cameron 1993). However, more elaborate forms of recruitment communication such as the honey bee waggle dance and stingless bee odor trails may have evolved from simpler behaviors that activated foragers without providing location information.

Bumble bees use multiple sensory modalities to trigger foraging. Tergal gland pheromone is sufficient to activate *B. terrestris* colony foraging (Dornhaus et al. 2003). Other modalities contribute. *Bombus terrestris* foragers may produce vibratory signals during foraging activation (Dornhaus and Chittka 2004; Oeynhausen and Kirchner 2001), and *B. impatiens* foragers contacted by a successful forager had an increased probability of exiting the nest to forage (Renner and Nieh 2008). Movements that stimulate colony foraging are not well understood. For example, the wing-fanning behavior of a successful forager could help disperse foraging activation pheromone: the higher the quality of the food source, the more wing-fanning motions *B. terrestris* foragers performed (Dornhaus and Chittka 2004). Foragers also spent more time moving at higher velocity inside the nest after collecting more profitable food (Dornhaus and Chittka 2005). Forager movements and nestmate contacts play a key role in honey bee recruitment dances (Rohrseitz and Tautz 1999) and in stingless bee recruitment (Barth et al. 2008; Hrncir et al. 2000; Schmidt et al. 2008).

We examined foraging activation in *B. occidentalis* Greene 1858, a species that can activate nestmate foraging (Wilson et al. 2006). Also known as the "western bumble bee," this species was once common in the western United States and western Canada, but has declined dramatically in western and central California, western Oregon, western Washington, and British Columbia (Thorpe 2005). Its decline may have been influenced by competition with invasive European honey bees (Thomson 2004) and disease (Rao and Stephen 2007; Whittington and Winston 2003). We sought to learn more about forager activation behavior inside the nest, using this species as a general model for bumble bee behavior. We conducted three experiments to test the effect of (1) food availability on foraging activation, (2) food quality on foraging behavior outside the nest, and (3) food quality on forager motions (path length and velocity) inside the nest.

Materials and Methods

We purchased four *B. occidentalis* colonies from Biobest Corporation (Leamington, Ontario, Canada). We used colonies 1 and 2 from September-December 2003, colony 3 from September-December 2004, and colony 4 from January-March 2005. Each colony

contained approximately 100–200 workers. We conducted our experiments at the University of California San Diego, La Jolla, California, USA (N09°09.890′, W79° 50.201′). Colonies developed normally and showed no signs of disease. Each colony was housed inside a nest box (42 long×24 wide×15 cm high, 2 cm thick walls, total interior area=88 cm^2) with wood floor and walls. The nest was covered with a clear plastic sheet and a wood cover for darkness when not under observation. We removed all cotton from the nest to provide a clear view of nest behavior and kept the room at 30°C for colony warmth. On one side of the box, a clear vinyl tube (16 cm long by 3 cm diameter) connected the nest to the foraging arena, a plastic enclosure (81 long× 34 wide×32 cm high) covered in clear plastic. Inside the foraging arena, bees collected nectar from a shallow plastic dish (2 ml volume) provided ad libitum with unscented sucrose solution. Nectar collected by bumble bees from six floral species at multiple field sites varied in concentration from 16% to 48% (mean of 37.8%, Pleasants 1981). We therefore used unscented sucrose solutions (Ultra Pure #821721, ICN Biomedicals, Irvine, California, USA) prepared in double-distilled water at concentrations of 0.5, 1.0, and 2.5 M (16%, 31% and 65% w/w, conversions from Kearns and Inouye 1993).

We conducted one foraging trial per day, beginning at 09:30 and ending before 11:00. Trials were not conducted on consecutive days. From 16:00 to 18:00, we provided *ad libitum* (unlimited) freshly ground pollen (collected by honey bees, stored frozen until use) in the foraging arena. We deprived the colony of sucrose on the day before each trial. Inside the colony, honey pots were always at least 50% full. The arena was illuminated with a 50 W halogen lamp (color temperature=3,200 K, 06:00–18:00). We used numbered plastic tags (Bee Works, Orillia, Ontario, Canada) to mark all bees (captured and tagged without chilling, Wilson et al. 2006).

Experiment 1: Effect of Food Quality on Colony Foraging Activation

Colonies 1 and 2 were used to test the effect of food quality (unscented 0.5, 1.0, and 2.5 M sucrose solutions) on foraging behavior (23 trials). We randomly selected one sucrose concentration per trial and provided it for 30 min. To measure foraging activation, we counted the number of bees entering the foraging arena every 2 min for 30 min *before* sucrose solution was available and 30 min *after* sucrose solution was removed ($\Delta bees_{entering}$). For each trial, we calculated a single value, the mean 2 min census count in the after phase minus the before phase. We also measured the time individuals spent collecting sucrose.

Experiment 2: Effect of Food Quality on Forager Behavior inside the Nest

Colonies 1–4 were used to determine the effect of food quality (unscented 0.5, 1.0, and 2.5 M sucrose solutions) on the within-nest behavior of active foragers (134 trials). Only one sucrose concentration (randomly selected out of three) was presented per trial. We provided ad libitum sucrose in the foraging arena for 60 min, randomly selected a bee collecting food, and waited for her return to the nest. If she did not return within 15 min, we chose a different bee. Bees that stayed in the nest for more than 5 min tended to stop foraging. We were interested in actively foraging bees because their behavior is more likely relevant to foraging activation. Thus, we only analyzed the movements of individuals who spent less than 5 min inside the nest before departing to forage again.

We recorded focal bee motions inside the nest (illuminated with a 20 W halogen light, no evident disturbance effects) with a digital video camera (Panasonic model PV-DV402D, Secaucus, New Jersey, USA). Videopoint v1.0 (Lenox software, Lenox, Massachusetts, USA) running on an eMac (Apple Computer, Cupertino, California, USA) was used to digitize forager motions. We used Excel v12.2.0 (Microsoft Corporation, Redmond, Washington, USA) to calculate the total path length (the sum of distances between successive points measured each 0.1 s) and forager velocity (calculated each 0.1 s). *Bombus terrestris* foragers spent more time at high velocities (≥4 cm/s) after feeding at 2.0 as compared to 0.5 M sucrose (Dornhaus and Chittka 2005). We therefore tested the effect of sucrose concentration on the amount of time that *B. occidentalis* foragers spent at high velocities, defining high velocity as ≥4 cm/s to facilitate comparisons.

Statistical Analysis

We used JMP v4.0.4 statistical software to analyze our results. The data met assumptions of parametric tests as determined through residual analyses. For *experiment 1*, we conducted repeated-measures Analysis of Variance with colony as a repeated measure and sucrose concentration and $\Delta bees_{entering}$ (log transformed) as fixed factors. In *experiment 2*, we focused on individual forager behavior, not the level of colony foraging activation. To eliminate pseudoreplication, we used each forager only once, and obtained a single value per forager for each measurement used in our analysis (time spent collecting sucrose, time inside nest, path length, mean velocity for her entire visit inside the nest, and mean velocity for the part of her visit in which she moved at ≥4 cm/s). We log transformed all of these measurements. We treated colony as a random effect (Standard Least Squares analysis of variance with REML algorithm). We report mean±1 standard deviation (S.D.). Where appropriate, we applied a Sequential Bonferroni correction (Zar 1984) for multiple tests on the same data. Tests that pass the correction are reported as "$*^{SB}$".

Results

Experiment 1: Effect of Food Quality on Foraging Activation

Bees foraged at all three sucrose concentrations, spending 61±111 s outside the nest after collecting sucrose and then 235±200 s inside the nest. There was an effect of sucrose concentration on foraging activation (Fig. 1). More bees entered the foraging arena after as compared to before food was available, (full model: $F_{3,19}$=3.68, P=0.030; sucrose effect: $F_{2,19}$=4.12, P=0.033; repeated-measures colony effect: $F_{1,19}$=0.19, P=0.664). For all sucrose concentrations, the mean increase in the number of foragers is positive (≥0.7 bees per 2 min census period). Although there was substantial variation in the number of bees entering the foraging arena, the increase in foraging was on average 2.8 and 3.6 fold greater for 2.5 M sucrose as compared to 0.5 M and 1.0 M sucrose, respectively. There was little difference between the increase in foraging for 0.5 M (0.9 foragers/2 min) and 1.0 M (0.7 foragers/2 min) sucrose (Fig. 1).

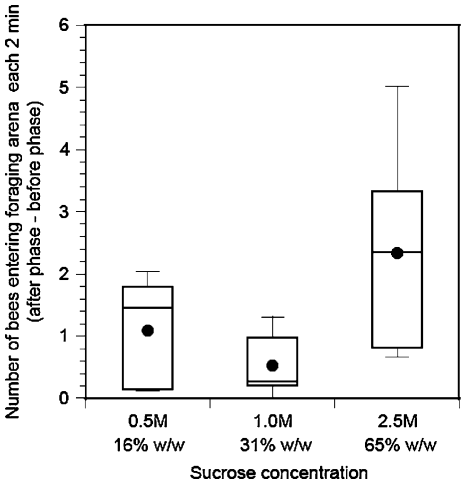

Fig. 1 The effect of sucrose concentration on colony foraging activation. The data for both colonies is pooled because there was no significant repeated-measures colony effect (P=0.66). Quartile box plots show the distribution of $\Delta bees_{entering}$ (difference between the number of bees entering the foraging arena in the after phase and before phase) at each sucrose concentration. The mean±SD values for the number of foragers entering the foraging arena after food was present are 0.9±0.6, 0.7 ±0.5, ands 2.5±2.1 bees each 2 min for 0.5, 1.0, and 2.5 M sucrose solution respectively

Experiment 2: Effect of Food Quality on Forager Behavior inside the Nest

Successful foragers returned to the nest, stored their food, and in many cases appeared to run excitedly around the nest. We rarely observed wing-fanning by foragers, and therefore focused on the paths made by foragers inside the nest (64 of these typical paths are shown in Fig. 2a). Out of the 159 foragers from four colonies that collected nectar in the foraging arena, only 134 returned to the nest immediately after foraging. The remainder stayed in the foraging arena for several hours and their subsequent behavior in the nest was not analyzed.

There was a significant effect of sucrose concentration on the time bees spent taking up sucrose (n=159 bees, sucrose effect: $F_{1,156}$=279.1, P<0.0001; colony accounted for less than 1% of model variance, Fig. 2b). On average, foragers spent an additional 57 s collecting per 1 M increase in sucrose concentration (Fig. 2b). There was no significant effect of sucrose concentration on time spent inside the nest ($F_{1,47}$=3.66, P=0.062, colony accounted for 3% of model variance). Foragers spent 93.9±75.4, 142.5±98.9, and 173.7±79.1 s inside the nest after returning from 0.5, 1.0 and 2.5 M sucrose solutions, respectively.

There was no significant effect of sucrose on average forager velocity inside the nest ($F_{1,95}$=3.04, P=0.085, colony accounted for 7% of model variance). Mean velocities were 2.3±1.3, 1.9±1.0, and 1.5±0.7 cm/s for 0.5, 1.0 and 2.5 M sucrose solutions, respectively. However, forager path length increased with increasing sucrose concentration ($F_{1,125}$=5.94, P=0.016*^{SB}, colony accounted for 14% of model variance, Fig. 2c). Mean path lengths were 145±93, 210±164, and 235± 131 cm for 0.5, 1.0, and 2.5 M sucrose respectively.

On average, foragers moved at high velocities (≥4 cm/s, a speed chosen to enable comparison with *B. terrestris*, Dornhaus and Chittka 2005) for 6% of their time inside the nest (over all sucrose concentrations). When a forager moved inside the nest at velocities ≥4 cm/s, there was no significant effect of sucrose concentration on time spent inside the nest ($F_{1,44}$=0.001, P=0.97, colony accounted for 2% of model variance), average velocity ($F_{1,108}$=0.08, P=0.78, colony accounted for 8% of model

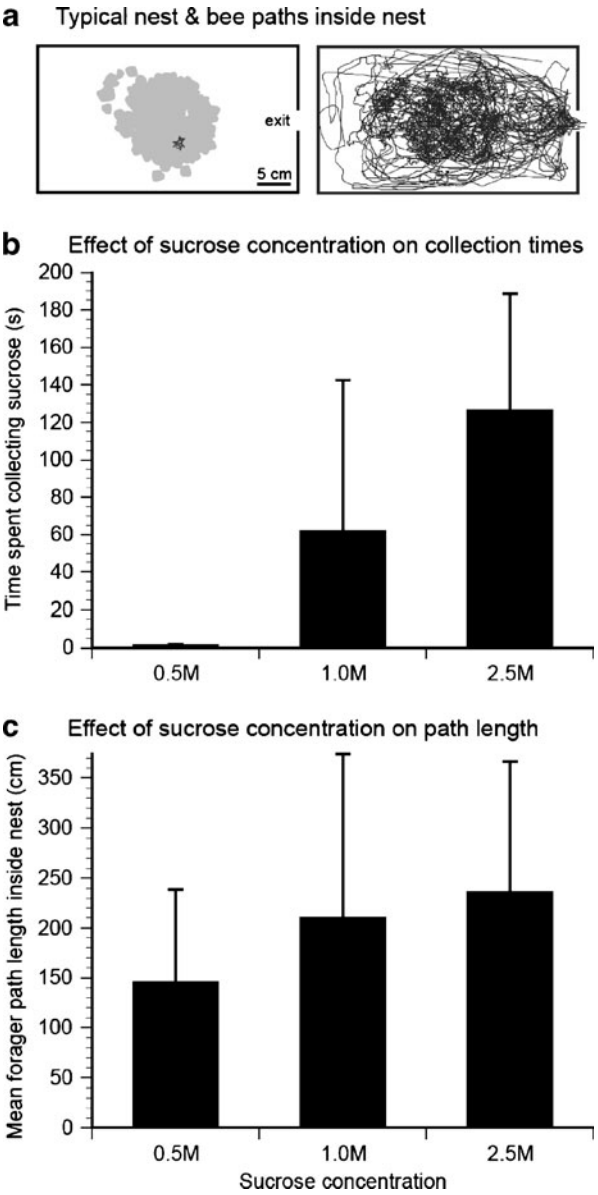

Fig. 2 Effect of sucrose concentration on forager behavior inside the nest. **a** Schematic of typical nest (grey structures are food storage pots and brood cells) and the paths of 64 foragers returning from collecting 2.5 M sucrose solution. **b** Time spent collecting sucrose (n=46, 49, and 64 bees for 0.5, 1.0, and 2.5 M sucrose respectively, error bars show standard deviations). **c** Path length of foragers inside the nest (n=21, 49, and 64 bees for 0.5, 1.0, and 2.5 M sucrose respectively, error bars show standard deviations)

variance), or path length ($F_{1,8}$=0.011, P=0.92, colony accounted for less than 1% of model variance).

Discussion

Bombus occidentalis colonies activated foraging by allocating more foragers to more calorically rewarding sugar solutions. The number of bees entering the foraging

arena significantly increased for higher concentration sucrose solutions (Fig. 1). Foragers spent significantly more time imbibing higher sucrose concentration solutions (Fig. 2b). Foragers then returned to the nest where they moved in elaborate paths at variable speeds (maximum of 5.0 cm/s) throughout the nest (sample paths shown in Fig. 2a). There was no significant effect of sucrose concentration on average forager velocity or time spent inside the nest. However, the length of a forager's path inside the nest (total of all distances moved each 0.1 s) significantly increased with sucrose concentration. On average, individuals foraging on 2.5 M and 1.0 M foragers walked paths respectively 1.6 and 1.4 fold longer than the paths of individuals foraging on 0.5 M solution (Fig. 2c).

Foraging Activation

A previous study of *B. occidentalis* foraging reported an increase of 1.6 bees/min entering the foraging arena after one forager returned to the colony with 2.5 M sucrose (Wilson et al. 2006). We provided the colony with unrestricted access to sucrose for 30 min before removing the sucrose and measuring foraging activation. Thus, it is not surprising that we recorded a higher mean rate of 2.5 bees/min after 2.5 M sucrose was available (Fig. 1). The number of *B. occidentalis* foragers entering the foraging arena was on average 2.8 and 3.6 fold greater for 2.5 M sucrose as compared to 0.5 M and 1.0 M sucrose, respectively.

Foraging activation for the lower concentrations (0.5 M and 1.0 M solutions) was similar (Fig. 1). Although 1.0 M is a fairly concentrated sucrose solution (31% w/w), it did not elicit more foraging than 0.5 M sucrose solution, perhaps because colonies had fairly high carbohydrates reserves (>50% of honey pots full) from the 2.5 M solution provided ad libitum for 30 min in some trials. In *B. terrestris*, foraging activation in response to nectar influx is greater when colony nectar stores are empty as compared to full (Dornhaus and Chittka 2005)

By comparison, *B. transversalis* foraging activity increased by 1.6 fold (on average) when one forager was allowed to return with collected food as compared to the control no-food phase (Dornhaus and Cameron 2003). *Bombus terrestris* foraging activity increased by several fold when all foragers were allowed to collect food (Dornhaus et al. 2003). It would be useful to compare our results with foraging activation in free flying *B. occidentalis* colonies. Unfortunately, this species is increasingly difficult to find and may be endangered (Thorpe 2005).

Nectar Imbibing Times

In the field, wild *B. occidentalis* foragers collecting nectar from *Erythronium grandiflorum* spent more time visiting flowers with more concentrated nectar (0.38–1.8 M sucrose, Thomson 1986). We similarly found that foragers spent more time collecting higher concentration sucrose (Fig. 2b). Time spent collecting sucrose is affected by the increasing viscosity of higher concentration sucrose solutions and the total volume collected per forager. Harder (1986) studied the ingestion rate of *B. fervidus*, *B. impatiens*, and *B. vagans* and found no changes in ingestion rates at concentrations from 10% to 50% w/w, but a significant decline in ingestion rate (going from 1.6 μl/s to 0.88 μl/s) for 65% w/w sucrose. Thus, for an equal volume, a

2.5 M sucrose solution would require 1.8 times longer to imbibe than a 0.5 M (16% w/w) or a 1.0 M (31% w/w) sucrose solution.

Bombus occidentalis foragers spent 1.0±0.5, 61.6±81, and 125.9±62.7 s collecting 0.5, 1.0 and 2.5 M sucrose solutions, respectively (Fig. 2b). Foragers only sampled (for 1 s) but likely did not collect any significant quantity of 0.5 M sucrose. In our experiment, foragers spent twice as much time collecting 2.5 M as compared to 1.0 M sucrose, close to the 1.8 fold difference calculated by Harder (1986) for imbibing times in other species. This suggests that differences in viscosity, not total volume collected per forager, may account for our collection time differences. However, this question requires further study. Similar correlations between sucrose solution concentration and imbibing times are also observed in stingless bees and honey bees (Roubik and Buchmann 1984).

Forager Movements in the Nest

Species-specific differences may exist between the within-nest behavior of *B. occidentalis* (our study) and *B. terrestris*. *Bombus occidentalis* significantly increased path length inside the nest when returning from higher quality sucrose solution. Bees returning from richer food had a weak (non-significant, $P=0.06$) tendency to spend more time inside the nest, increasing from 93.9 s to 173.7 s for 0.5 M and 2.5 M sucrose solutions, respectively. Bees also did not move at a constant speed inside the nest. Thus, the combined effects of time spent inside the nest and variable velocities may have contributed to the significant increase in path length for bees returning from higher concentration sucrose solution.

We found no effect of sucrose concentration on time spent inside the nest, average velocity, and path length when *B. occidentalis* foragers moved at velocities ≥4 cm/s. In contrast, *Bombus terrestris* foragers spent more time per nest visit moving at high velocity (≥4 cm/s) after returning from 2.0 M as compared to 0.5 M sucrose (Dornhaus and Chittka 2005). We also did not observe much wing-fanning by returning foragers inside the nest at any sucrose concentration, unlike B. *terrestris*, which exhibits such wing-fanning (Dornhaus and Chittka 2005).

Species differences are not surprising given that *B. occidentalis* and *B. terrestris* are relatively distant from each other on the phylogenetic tree of the genus *Bombus*. Both species are separated by several nodes (Cameron et al. 2007). For *B. occidentalis*, the longer paths of foragers returning from higher quality (more calorically concentrated) food could result in a greater number of nestmate contacts, a factor shown to be important in the activation of *B. impatiens* foragers (Renner and Nieh 2008) and that is also observed in *B. terrestris* foragers (Dornhaus and Chittka 2001). Bumble bees, unlike honey bees, do not recruit nestmates with stereotyped dance behavior (Dornhaus and Chittka 2004). However, our results show that there is variation in how successful foragers of different bumble bee species move and activate foraging inside the nest. A detailed investigation of wing-fanning, movement velocities, and path length among different species, when mapped onto the phylogeny, would provide a better understanding of how foraging activation has evolved in *Bombus* and contribute to our understanding of the evolution of such information transfer in the corbiculate bees.

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