
Original article

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The food recruitment dance of the stingless bee, *Melipona panamica*

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Abstract Foragers of the stingless bee *Melipona panamica* can communicate the location of a good food source to nestmates and evidently communicate part of this information inside the nest. However there is no careful description of within-nest recruitment behavior for this species or for any other stingless bee. Therefore the goal of this paper is to provide a detailed description of the behaviors of recruiting *M. panamica* foragers within the nest. A recruiting forager enters the nest, begins producing pulsed sounds as food-unloading bees collect her food (unloading phase), and then performs a dance by rapidly executing clockwise and counterclockwise turns while continuing to produce sound pulses (dance phase). To investigate whether directional information is encoded in the dance, I alternately recorded the behavior of foragers trained to two food sources, each 175 m from the colony but in opposite directions (north and south). I examined the following parameters and found no differences between the dances of foragers feeding in opposite directions: (1) order of clockwise and counterclockwise turns, (2) turn direction, (3) angular start position, (4) angular stop position, (5) turn magnitude, and (6) turn angular velocity. Foragers recruiting for a rich food source (2.5 M) initially unloaded food with their bodies oriented 180° from the entrance. They began turns at random orientations, but tended to end these turns facing the nest entrance (0°). Dancers for poor food sources (1.0 M sucrose solution) turned at significantly lower velocities than dancers for good food sources (2.5 M sucrose solution), and exhibited random initial, start-turn, and stop-turn orientations. Throughout her stay inside the nest, the recruiting forager produced sounds. During sound production, her folded wings vibrated dorsoventrally over her abdomen and she attracted the attention of follower bees who

positioned their antennae closely around her body. Foragers recruiting for 1.0 M and 2.5 M food sources attracted the same number of food-unloading bees, but 1.0 M recruiters attracted significantly fewer followers around their abdomens.

Key words Stingless bees · *Melipona panamica* · Communication · Dance Sounds

Introduction

Recruitment is a process in which a single bee discovers a resource outside the nest and advertises the existence of this food source to nestmates. This process is relatively well understood in the honey bees, however much remains to be learned about the recruitment of stingless bees (Meliponinae). Many stingless bees produce movements and sounds inside the nest after returning from a good food source, and these sounds may indicate the distance to the food source in some species (Lindauer and Kerr 1958, 1960; Esch et al. 1965; Esch 1967; Nieh and Roubik 1995). Lindauer and Kerr (1958, 1960) worked with several Brazilian species, including *Melipona quadrifasciata* and *M. scutellaris*, and provided a tantalizing glimpse of what occurs: “Until the first bees reached the feeding table, the bees in the nest were quiet, inactive and scattered about. But they started running around excitedly when the first bees returned from the feeder. These returning bees gave small amounts of syrup to the bees in the nest; very often they stopped doing this to run irregularly in zigzags in all directions, trying to jostle bees which were in their way....Now and then the zigzag run was interrupted by a sharp turn in a semicircle; then the bee gave up another portion of syrup and immediately continued the zigzag movement.” (Lindauer and Kerr 1960, p. 33).

The authors observed these “zigzag” movements in several other stingless bee species, but did not examine this behavior in detail. Thus the goal of this paper is to

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provide a careful and quantitative description of recruitment behavior in a stingless bee by documenting how a *M. panamica* forager behaves inside the nest after returning from a good food source.

I chose *M. panamica* because of the complexity of its recruitment system. A previous paper (Nieh and Roubik 1995) described the phenomenon of recruitment, using paired feeder experiments modeled after the designs of von Frisch (1967) and Lindauer and Kerr (1958) to establish that *M. panamica* foragers can communicate the direction, distance, and height above ground of a food source. Potential mechanisms for the communication of height and distance are presented in Nieh and Roubik (in press) however, these mechanisms can only be understood in light of a complete and detailed description of the recruiting forager's behavior. Therefore, this paper (1) describes where a forager recruits inside the nest and how she orients while recruiting; (2) examines the zigzag turns produced during her dance for specific patterns of turn direction, start position, stop position, turn magnitude, and turn velocity; (3) tests if these aspects of the dance are correlated with the direction of the food source from the nest; (4) describes the sounds produced in the dance; (5) describes where followers position their antennae around the dancer, and (6) describes how the dance changes with shifts in food quality (sucrose concentration).

Methods

Study site and bee colony

I conducted these studies from August to November 1992 and 1995 in the seasonal tropical moist forest on Barro Colorado Island (Lake Gatun, Panama). I used two colonies of *M. panamica* (colonies A and B) obtained from natural wood log nests from the Santa Rita Ridge region (approximately 15 km southwest of Portobello, Colon Province, Panama). Both colonies were transferred into wooden observation nests. Each nest contained three interconnected chambers (Fig. 1). The deepest chamber held the brood comb. The shallower second chamber held honey pots and pollen pots. The triangular third chamber was 6.4 mm deep and gradually tapered in width to a point from which a vinyl tube (1 cm inner diameter) allowed bees to exit and enter the nest. Foraging bees unloaded their food and performed recruitment behavior in this chamber, and observations were made through the plate glass covering the top face of the nest. Further details on the design of this nest are given in Nieh and Roubik (1995).

For all experiments, I placed the nest at a tilted angle inside a laboratory building such that the nest's long axis was 35° from the horizontal, and the nest entrance was inserted through a window (Fig. 1). To reduce the disturbing effects of light, the area around the nest was enclosed with a velvet curtain and the laboratory windows were covered with aluminum foil.

Training

Foragers were trained from the nest to a grooved-plate sucrose solution feeder consisting of a 60-ml Kimax glass recrystallization dish inverted over a clear grooved Lucite disk. I dispensed 100 μ l of anise scent onto a 4.9-cm² wedge of filter paper placed on top of the glass dish. The food itself was also scented with 1 μ l anise scent/ml

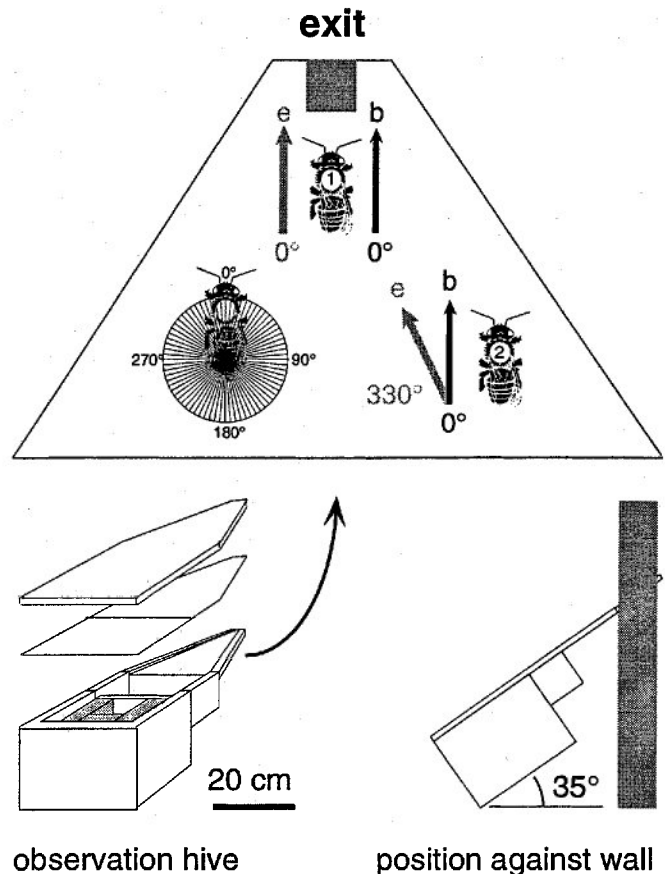


Fig. 1 Method for obtaining angular measurements of forager positions inside the nest. The lower portion of the figure shows a scheme of the three-chambered observation nest and how it was placed against the wall. The unloading platform (trapezoidal area) is depicted in the upper portion of the figure. The gray square represents the nest exit (a Tygon tube). The exit vector (*e*, vector from the tip of the forager's abdomen to the nest exit) is shown in gray and the body vector (*b*, vector from the tip of the forager's abdomen to her head) is shown in black. These angles were measured by placing a clear acetate compass (shown lower left) over the videotaped body of the forager such that 0° pointed directly upwards. In this figure, forager 1 is facing the nest exit and is positioned along the nest midline. Thus her exit angle and her body angle are both 0°, and the corresponding difference angle (the smallest angular difference between the exit and vertical angles) is 0°. Forager 2 also has a body angle of 0°. However, her exit angle is 330°, and thus her difference angle is 330°. For purposes of illustration, foragers are shown larger than normal relative to the unloading platform

of solution. The feeder was placed at the center of a plastic stand sitting inside a saucer containing water (to exclude ants).

Bees were trained by initially presenting the feeder near the nest entrance, waiting for a few bees to feed, and then gradually moving the feeder further away in the desired direction (method of von Frisch 1967). To train bees across water, the feeder was placed inside a canoe and gradually paddled across the lake to a floating 4 × 4 m raft. Powdered paint pigments suspended in shellac were used to mark each visiting forager with a unique combination of colors on the thorax and abdomen. For the videotaped dance observations, bees were marked with numbered tags glued on the thorax (Opalith-Zeichenplättchen). Both marking methods are highly reliable (von Frisch 1967). The number of foragers arriving in each 15-min interval was censused. To maintain a constant number of foragers at the feeder, I censused the number of foragers arriving in each 15-min interval and captured or released marked

foragers as necessary. Assistants captured all bees in Ziploc plastic freezer bags to limit the potential release of alarm pheromone (method discussed in Gould et al. 1970).

I define "newcomers" as bees that were not trained to the feeder and that consequently must have found the feeder through a random or a directed search. I identified newcomers as bees that were unmarked. All bees were uniquely marked with shellac paints as soon as they landed on the feeder during the training and experimental phases. My assistants radioed in these color marks, and I checked inside the nest to verify that these bees had returned. Any bees that did not return to the colony under observation were presumed to come from other colonies and were immediately captured in plastic bags and killed upon their next return to the feeder.

Feeders

To examine recruitment over a body of water, bees from colony A (located on the shore) were trained to a floating platform 250 m east of the nest in Lab Cove by Slothia Island. Water completely surrounded this platform for at least 100 m in all directions. The bees foraged at a 2.5 M anise-scented sucrose solution.

To examine the dance for directional components, I trained one group of foragers to a feeder 175 m south of colony B and a second group to a feeder 175 m north of colony B. Both feeders were located in the forest at approximately the same altitude, were identical, and contained equal volumes of sugar solution. However in some experiments, the south feeder contained 1.0 M sucrose solution while the north feeder contained 2.5 M sucrose solution. All solutions contained 1 μ l anise scent/ml sugar solution. Every 60 min, assistants used calibrated syringes to simultaneously dispense 100 μ l of anise scent onto the filter paper on top of each feeder (coordinated with two-way radios).

When testing for the effect of decreasing sucrose concentration, 2.5 M and 1.0 M sucrose solution were alternately provided at the south feeder. The north feeder always contained 2.5 M sucrose solution. For simplicity, bees feeding at the north feeder will be referred to as "north foragers" and bees feeding at the south feeder as "south foragers." Similarly, bees feeding at a 1.0 M sucrose solution are "1.0 M foragers", and bees feeding at a 2.5 M sucrose solution are "2.5 M foragers."

Observations of behavior inside the nest

I videotaped the behaviors of colony B foragers, alternately recording a south forager and then a north forager. This comparison controlled for behavioral changes imposed by the environment since such changes should have simultaneously affected both groups. To limit overlap between the performances of foragers inside the nest, only two foragers at a time were allowed to feed at each feeder. All other foragers were captured. Periodically, the assistants released a new pair of marked foragers and captured the old pair to allow observations on a new set of foragers.

Select portions of the unloading platform were illuminated with a Bausch & Lomb Fiber-lite. The honey pots and brood comb were not illuminated. This cool, yet bright, light source did not appear to disrupt normal behavior inside the nest. Bees unloaded food, recruited, and did not try to fly towards the artificial light as they exited. Their behavior appeared identical to that observed under a bright-red LED light source (gallium-aluminum-arsenide light-emitting diode) generating negligible amounts of heat with a peak intensity around 667 nm and filtered to pass only wavelengths longer than 640 nm (Roscolux medium red filter no. 27). The photoreceptors of *M. marginata* and *M. quadrifasciata* workers are insensitive to light at these wavelengths (Hertel and Ventura 1985).

I videotaped the behavior and distribution of bees on the food unloading platform with a Canon L-1 Hi-8 camcorder with hybrid analog-digital sound recording, manual gain, and VU meter. A ruled 3-cm card placed above the entrance enabled me to scale the video images for later analysis. Bee motions and sounds were re-

corded simultaneously. I also photographed forager behavior and scanned the resulting slides to produce figure templates.

The bees were exceptionally sensitive to air current disturbances, and thus the microphone could not be moved to maintain a constant forager-to-microphone distance (to measure sound amplitude levels). Instead, a microphone was placed 5 cm down from the nest entrance. Most foragers performed their recruitment behavior within 4–5 cm of the microphone. I was able to obtain fairly clear recordings of individual foragers by limiting the number of foragers at each feeder and recording only on days when foraging activity for natural food sources was quite low. The microphone consisted of a Teflon tube (4.5 cm long, 1.7 mm inner diameter) inserted into the nest and connected to a Radio Shack electret condenser microphone (catalog no. 33-1052) outside the nest. This inexpensive microphone has excellent frequency response characteristics (Bennet-Clark 1997; Fonseca and Bennet-Clark, in press). The microphone output was connected directly to the video camera. This video camera had a flat frequency response from 75 Hz to 10,000 Hz, and the microphone had a relatively flat frequency response from 50 Hz to 7,000 Hz with the exception of two resonance peaks at 750 Hz and 3 KHz (respectively 11 dB and 6 dB over the average frequency response). The video camera was calibrated by directly connecting the output of a Beckman Industrial function generator (model FG2 A) into the video camera microphone input (gain set to 1) and then recording the sine waves onto a videotape. I then played back the videotape and compared the recorded with the original sine wave amplitudes using a Protek P-2820 20 MHz oscilloscope. The Radio Shack microphone was calibrated by mounting it and a B & K probe microphone (type 4182) with a known frequency response from 20 to 20,000 Hz at a distance 15 cm away from a loudspeaker. The entire setup was placed in an anechoic chamber and I then compared both microphone outputs using the Protek oscilloscope.

Motion analysis

I copied the Hi-8 tapes onto VHS tapes and then used a JVC BR-S525U videocassette player to analyze the distribution of bees on the unloading platform and to view the dances in slow motion. Antennal positions, bee positions, and calibration units were marked onto acetate sheets and scanned for analysis with a Macintosh Quadra 800 computer. All image sizes were equalized according to the calibration marks with the program Canvas v3.5.

To analyze the dancers' angular positions, I used a 6.8-cm acetate disk ruled in 5° increments. Because the nest was sloped 35° from the horizontal (Fig. 1), angles were measured relative to the vertical (gravity) as well as relative to the nest exit. I centered the disk on the posterior tip of the dancer's abdomen and measured the angle of the dancer's longitudinal axis relative to a line parallel to the long axis of the nest (body angle) and the angle to the nest exit (exit angle, Fig. 1). I then calculated a difference angle (the angular difference between the body angle and the exit angle). Thus a forager whose body points directly towards the nest exit always has a exit angle of 0° regardless of her position on the unloading platform. However, her body angle will vary with her position on the unloading platform.

The movements of each dancer were viewed frame by frame (at 30 frames per second), and I recorded (1) her initial position as she unloaded food to other bees, (2) the position at which she began to turn, (3) the position at which she stopped turning, (4) the amount of time she spent in making each turn (as calculated from the video frames), and (5) whether she made a clockwise or a counterclockwise turn. One complete turning movement was defined as a movement of the bee's longitudinal axis either clockwise or counterclockwise without a pause greater than 0.1 s (three video frames). This time interval was the smallest pause in movement that could be detected reliably with the video playback system. From these data, I additionally calculated (6) the number of degrees turned and (7) her angular velocity. I also traced her path during the dance phase (from the position of her thorax taken each 0.033 s) along with calibration marks onto acetate sheets, scanned

these sheets into the computer, and used Canvas v3.5 to trace these paths and measure path lengths. To obtain (8) her average velocity, path length was divided by the amount of time taken to traverse this path.

Analysis of turn order

To determine if the sequence of clockwise (c) and counterclockwise (ccw) turns was non-random, I performed a goodness-of-fit analysis as follows. In a sequence with two turns, there are four possible combinations: (c, c) (c, ccw) (ccw, c) (ccw, ccw). Observed values for these tests were obtained by counting the number of sequences that fell under each of these combinations. Pairwise tests were then performed to compare the first and the second turn, the first and the third turn, the second and the third turn, etc. These tests address the question, "Given that the *i*th turn is *x*, is the *j*th turn likely to be *y*?" By summing the individual *G*-tests, I then tested the complete sequences for overall non-randomness (Sokal and Rohlf 1981). A runs test was not used because this would require sequences containing at least ten turns, and a maximum of eight turns was observed during any one sequence.

Analysis of turn angles, angular velocity, and average velocity

The distributions of the initial food-unloading angles and dance angles were analyzed by first determining which distributions were significantly non-random (Rayleigh test, Greenwood and Durand 1955). For each non-random distribution, I tested if the direction of the mean vector equaled 0° or 180°, as appropriate, with Stephens' (1962a) "polar vector" test. Finally, I used a modified *F*-test (described by Stephens 1962b) to determine if the mean vector magnitudes and the variances of the two error distributions were significantly different. Although parametric, this test is robust even for a violation of the assumption of circular normality (Stephens 1962b).

To compare inherently non-circular distributions (the distributions of degrees turned, the amount of time spent in making each turn, the angular velocity of each turn, and the average velocity of a dancer), I used a non-parametric test, the Mann-Whitney test (test-statistic *M*).

These analyses were repeated with data on bees foraging alternately from 2.5 M and 1.0 M sucrose solutions. For brevity, these solutions will be referred to as 2.5 M and 1.0 M.

Sound analysis

Dance sounds were digitized from the original Hi-8 tapes with a MacRecorder digitizer connected to a Macintosh Quadra 800 using the program SoundEdit v1.0 (sampling rate of 22.255 kHz, 8-bits). Only recordings in which a single recruiter was inside the nest were used. I analyzed these sounds with the program Canary v1.2.1 (Cornell Laboratory of Ornithology), generating FFT (Fast Fourier Transform) spectrograms and spectra. Sound pulse and inter-pulse data were measured from FFT spectrograms. I used a JVC BR-S525U videoplayer that allowed sound playback during slow-motion playback to synchronize sound changes with different phases of the foragers' behavior inside the nest.

Antennal positions

To quantify the antennal positions of bees orienting to recruiters, I traced the body outlines of recruiters onto acetate sheets (along with size calibration marks) and then marked antennal tip positions of attending bees (one dot for each antenna). A bee's antennae were only marked if the bee moved its head closer to the recruiter within 1 s of the recruiter moving within 1 cm (one bee length) of the recruiter's head. Such a small time interval was chosen in order to limit the analysis to bees that took an immediate interest in the recruiter. These orienting bees were classified into two groups:

followers and food-unloading bees. Foragers that brought in nectar or sugar solution unloaded it to other bees that stored it in the honey pots. Followers were bees which oriented to the forager but received no food or only very brief samples of food (≤ 1 s) from the recruiter. Food-unloading bees were bees which began to receive food from the recruiter immediately after orienting towards the recruiter. These bees also distinguished themselves by leaving and moving to other areas in the nest after receiving food. Followers that received food samples continued to orient towards the recruiter after receiving their food samples.

As the recruiter moved, I shifted the acetate for each video-frame to match her traced outline with her current position. I marked only the initial position of the orienting bee's antennae because I was interested in the regions of the dancer's body that initially attracted other bees. The subsequent antennal positions were not marked. Thus the antennal positions of all bees that oriented towards the dancer *during the entire time that the dancer was in the nest* are shown in Fig. 11. Since each bee had two antennae, half the total number of dots equals the number of orienting bees.

I distinguished between the antennae of bees that did and did not initially receive food from the dancer by marking the acetate with different colors. Some bees did not receive food upon their initial orientation towards the dancer but subsequently received food samples for brief periods of time. As before, the tracings were scanned into a computer and the size calibration marks were used to scale all tracings to the same size.

General statistics

The details of specific statistical tests have been discussed in the preceding sections. Throughout this paper, averages are reported as the mean \pm 1 SD. All tests are two-tailed. For groups of tests with $P > 0.05$, only the lowest *P*-value is reported. For individual tests with $P \leq 0.05$, I report the values of the test statistic, the degrees of freedom, and the *P*-value. When statistical tests are reported in tables, the main text gives only the *P*-values of major results.

Results

Recruitment

Figure 2 shows a typical buildup of foragers due to recruitment. By 9:45 a.m., I had trained one forager to a 2.5 M feeder on a raft 250 m from the shore, and at 10:15 a.m., the first newcomers arrived. Because no bees were removed from the feeder, the rate of recruitment was highest in the first 2 h (11 recruits) and then decreased during the next 2 h (three recruits) as the total number of foragers reached a plateau. The versatility of recruitment communication is shown in this buildup of nestmates to a site that bees would normally never visit (a small, barren raft in the middle of a bay).

Overview of foraging-related activity inside the nest

Inside the nest, foragers tended to move along a passageway constructed by the colony from mud and cerumen (a mixture of wax and resin). This passageway led from the nest entrance to the honey and pollen pot storage area. Active foragers continued to move preferentially through this area for several days after I had removed the limiting wall (Fig. 3A). One week after the

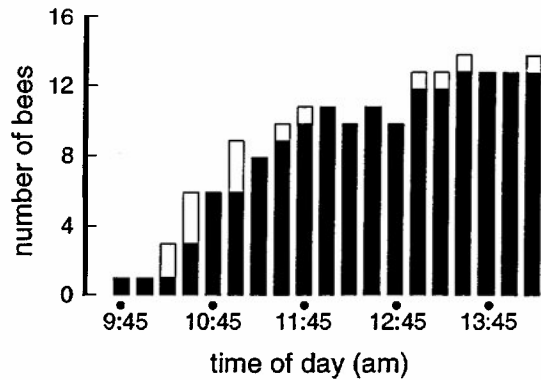


Fig. 2 The buildup of recruits to a feeder located on a raft in the center of a large body of water (censused in 15-min intervals). *Open bars* represent newcomers and *black bars* represent experienced foragers. Since all newcomers immediately became experienced foragers after they landed on the feeder, they are indicated in the black bars in the subsequent census interval. Foragers who found the feeder in previous time intervals (experienced foragers) did not necessarily return in all subsequent time intervals

data shown in Fig. 3 were collected, active foragers distributed themselves throughout the upper region of the platform, although they continued to be most concentrated in the region immediately adjacent to the exit. Upon entering the nest, most foragers were able to immediately find other bees to unload and store their collected sucrose solution. On average, a 2.5 M forager spent 35.9 ± 16.4 s inside the nest. She searched 4.0 ± 4.4 s before finding bees to unload her food, spent 25.0 ± 5.2 s unloading food, and 6.9 ± 1.4 s dancing ($n = 96$).

The initial unloading orientation of foragers returning from a 2.5 M food source, regardless of its direction, has a mean *difference* vector of 192° . This angle is not significantly different from 180° ($P > 0.085$, Fig. 3B, Table 1), and thus, on average, foragers were oriented directly opposite the nest exit when they initially unloaded their food.

Despite a fairly uniform distribution of inactive foragers and other bees throughout the unloading platform (Fig. 3C), most foragers unloaded their food in the area adjacent to the exit (Fig. 3B). The distribution of inactive foragers was similarly clustered around the exit (Fig. 3C).

The complete behavioral sequence of a recruiting forager is illustrated in Fig. 4. First, the forager (1) entered the nest and (2) found one or more bees to unload her food. This initiated the unloading phase. She began to produce pulsed sounds and continued to do so until her departure. She folded her wings over her abdomen and vibrated them dorsoventrally. She opened her mandibles and exuded a drop of nectar that unloading bees sucked with their tongues. Her abdomen visibly pulsated as she pumped out the nectar. During the unloading phase, she was stationary and other bees in the vicinity oriented towards her, often holding splayed antennae around her abdomen. After unloading her nectar, she began the dance phase. She began to spin,

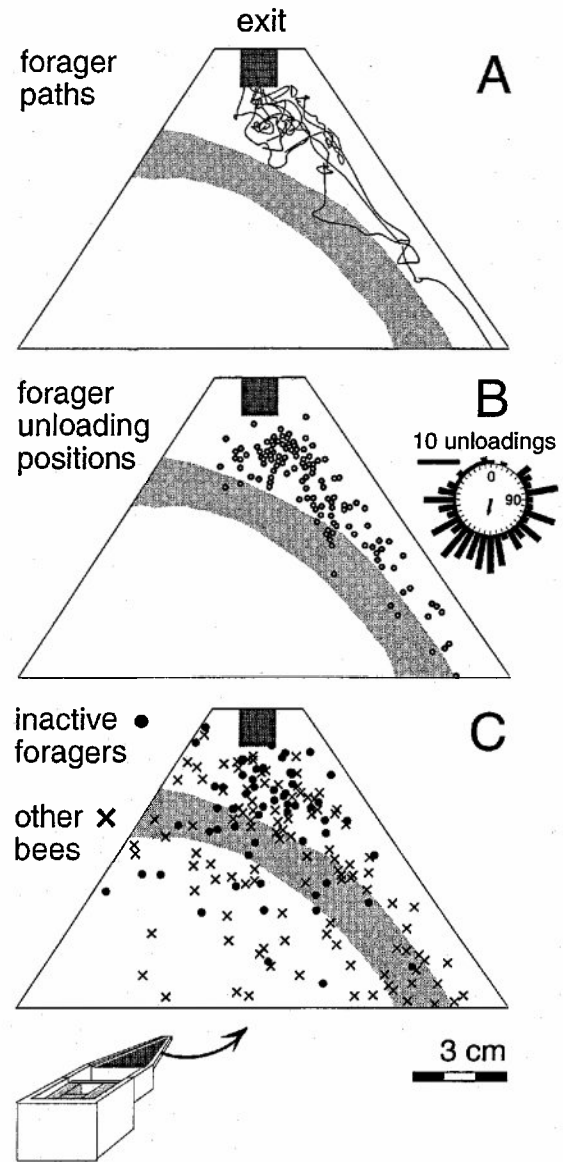


Fig. 3 The paths taken by walking foragers, their food unloading positions, and the positions of other bees on the unloading platforms. The *gray square* at the top of the trapezoidal unloading platform marks the vinyl tube through which bees could exit and enter the nest. The *gray curved band* represents the previous location of a wall of mud and cerumen (wax and resin) originally constructed by the bees to create a tunnel from the nest entrance to the food and honey pot storage chamber. Before the observations reported here, I removed the wall, but active foragers still limited their movements to its original boundaries during the next few days. **A** Paths made by five foragers. **B** Unloading positions of ten foragers (*open circles*) during multiple visits back to the nest. The circular distribution shows the long-axis orientation of foragers as they unloaded their food. (The *arrow* gives the mean vector direction and its length is proportional to the mean vector magnitude.) **C** Location of inactive foragers (*black circles* indicate foragers that had previously visited the feeder and received colored marks and tags, but which were not actively foraging during these observations) and all other bees (*crosses*). A small schematic of the complete observation nest is shown at the bottom of the figure with the unloading platform indicated in *gray*

turning (3) clockwise or (4) counterclockwise. Sound production continued. During these movements, the followers shifted their bodies and antennae to keep the

Table 1 Analysis of the distribution of clockwise (c) and counterclockwise (ccw) stop-difference angles for bees foraging at a 2.5 M sucrose solution at the north and south feeder. The distributions for both feeders were first analyzed separately and then combined. The distribution of initial unloading positions is also analyzed. The Raleigh test (Z) tests for non-uniformity of the distribution. Stephen's polar vector test is used to determine if the mean difference vector is significantly different from a specified direction. Stephen's modified *F*-test is used to test for significant differences between angular distributions of bees foraging at the north and south feeders

Turn direction	Stop-difference angles of bees from the:	Mean difference vector	<i>r</i>	<i>n</i>	Raleigh test (Z)	<i>P</i>	Mean vector different from:	<i>P</i>	Significant?	Distributions different? (<i>F</i> _{1,<i>n</i>-2})	<i>P</i>	Significant?
c	North feeder	20°	0.413	67	11.47	<0.0001	0°	> 0.065	No	0.015	0.902	No
	South feeder	18°	0.337	116	13.18	<0.0001	0°	> 0.060	No			
ccw	North feeder	356°	0.475	73	3.25	<0.0001	0°	> 0.850	No	0.139	0.709	No
	South feeder	353°	0.298	95	8.42	<0.001	0°	> 0.720	No			
c and ccw	North and south	8°	0.362	351	45.89	<0.0001	0°	> 0.120	No			
Initial unloading positions		192°	0.420	159	27.99	<0.0001	180°	> 0.085	No			

dancer within approximately 1 cm of their antennae. I defined a “follower” as a bee who oriented her body or antennae towards the dancer within 1 s of the forager moving within 1 cm of the follower. Because bees often initially oriented towards the recruiter during the unloading phase and continued to follow the recruiter during the dance phase, I will use the term “follower” and not “dance follower”. (5) The forager occasionally stopped and briefly offered food samples to followers. Between turns, she walked or ran around the unloading platform (Fig. 3A, 5). Upon leaving the nest, (6) she sometimes appeared to be followed by other bees.

Dance turns: clockwise (c) and counterclockwise (ccw) order

Figures 3A and 5 show the paths taken by recruiting foragers. As the foragers turned, they pivoted around the center of their long axis. This is most clearly shown in Fig. 6, where a forager performed four turns in the order c, ccw, c, c.

The distribution of clockwise and counterclockwise turns by turn order is given in Fig. 7. These results are based on an analysis of 123 trips back to the nest by nine individual foragers feeding at 2.5 M sucrose solutions (four from the north and five from the south feeder). I combined the data from north and south foragers because the pattern was identical when both directions were considered separately. Dancers were equally likely to turn clockwise or counterclockwise in their first five turns (Fig. 7). (Since the number of dancers making more than five turns was quite small, the sample size is insufficient for comparisons of the sixth through eighth turns.)

The randomness suggested by this distribution is borne out by the analysis of turn order. For north foragers, none of the eight *G*-tests revealed any significant order trends ($G_{\text{individual}} \leq 2.91$, $P \geq 0.09$), and there was no significant trend in overall order ($G_{\text{total}} = 4.89$, $P = 0.77$). For south foragers, three *G*-tests revealed no significant order trends ($G_{\text{individual}} \leq 2.31$, $P \geq 0.13$) and one *G*-test suggested that the second turn was more likely to be counterclockwise if the first turn was counterclockwise ($G_{\text{individual}} = 6.86$, $P = 0.01$). However, south foragers exhibited no significant overall order to their turns ($G_{\text{total}} = 1.29$, $P = 0.94$). Thus north and south foragers were equally likely to make clockwise or counterclockwise turns at any point in their sequence of turns.

Duration and speed of dance turns (for a 2.5 M food source)

These turn results are based on an analysis of 123 trips back to the nest by nine individual foragers feeding at 2.5 M sucrose solutions (four from the north and five from the south feeder).

Fig. 4 The behavior of a forager inside the nest after returning from a good food source. The behavior of forager 5-White is shown. She (1) entered the nest, (2) unloaded food and began to produce sounds, (3) stopped unloading food and made a clockwise turn, (4) made a counterclockwise turn, (5) paused to give the attending bee a food sample and then made a counterclockwise turn to face the exit, and (6) ran out of the nest entrance with the follower bee close behind

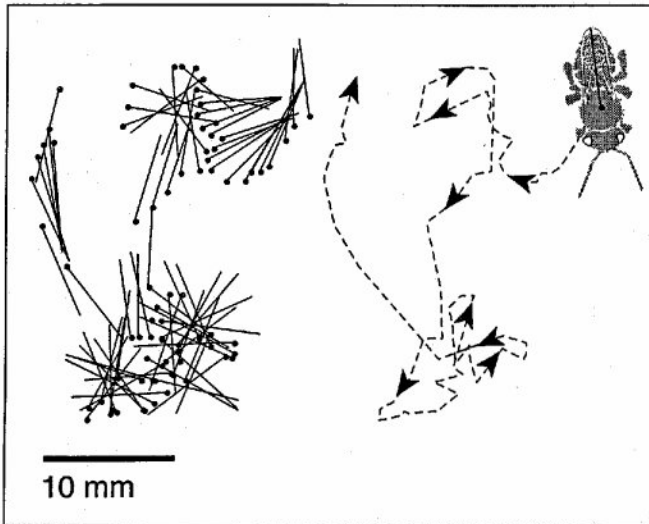
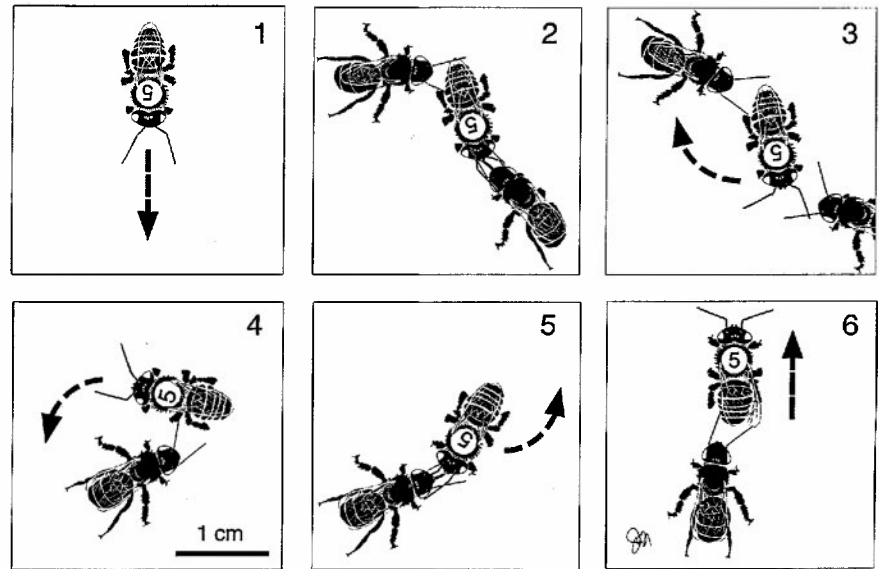


Fig. 5 The path taken by forager 7-Blue after returning from the north feeder with 2.5 M sucrose solution at 1:59 p.m. on 10 November 1995. The position of her body is shown each 0.1 s. For clarity, the path of her thorax (dashed line marked by arrows) and the position of her body are shown separately. A black dot marks the center of her thorax from which a line is drawn extending to the tip of her abdomen

The average number of degrees moved per turn was approximately the same for clockwise (c) and counterclockwise (ccw) turns. Considering c and ccw turns separately reveals that there is no significant difference between the number of degrees/turn for north foragers or south foragers during their movements clockwise or counterclockwise (four Mann-Whitney tests, $P \geq 0.26$). Pooling c and ccw turns reveals that bees foraging at the north feeder turned $214 \pm 89^\circ$, and bees foraging at the south feeder turned $231 \pm 115^\circ$ (no significant difference, $M_{155,158} = 23,667$, $P = 0.40$). The combined data from north and south dancers reveals that bees turned in the clockwise direction for $223 \pm 92^\circ$ and

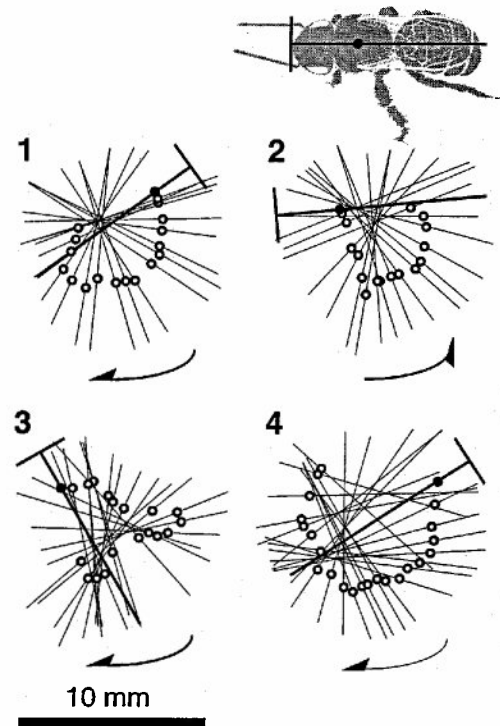


Fig. 6 Detail of dance turns. The position of forager 55-White's body is shown during the four turns that she made after returning from the south feeder (with 2.5 M sucrose solution at 10:19 a.m. on 10 November 1995). The position of her body is shown each 0.033 s. The long line indicates her longitudinal axis, the small bar indicates the anterior limit of her head, and a dot marks the center of her thorax. A black dot associated with a thicker line marks her thorax position at the start of each turn, and the open dots mark her subsequent thorax positions. Numbers and arrows indicate the order and direction of the turns

counterclockwise for $222 \pm 118^\circ$ (no significant difference, $M_{127,186} = 19,492$, $P = 0.57$, see Fig. 8). The mean number of degrees/turn for all data is $223 \pm 103^\circ$ (max. = 630° , min. = 5° , median = 220°).

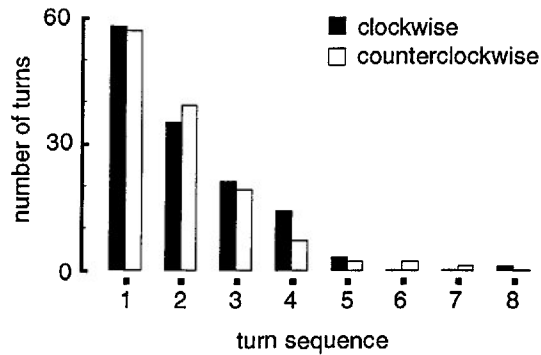


Fig. 7 Histogram of the number of clockwise (*black bars*) and counterclockwise (*open bars*) turns that nine individual foragers made during 123 trips back to the nest from a 2.5 M sucrose solution ($n = 259$ turns). This figure combines the data from the north and south feeders (four individuals from the north feeder and five from the south feeder)

With one exception, no significant differences exist between north and south dancers in terms of turn duration or turn direction (three Mann-Whitney tests, $P \geq 0.06$). The one exception is a significant difference for the duration of counterclockwise turns between the north and south dancers. South dancers took longer to make counterclockwise turns than north dancers (north turns = 0.65 ± 0.28 s, south turns = 0.84 ± 0.40 s; $M_{54,73} = 2882$, $P = 0.01$). However, the angular velocity of turns was the same for all groups (north and south, clockwise and counterclockwise; four Mann-Whitney tests, $P \geq 0.15$). The overall angular velocity was $341 \pm 155^\circ \text{s}^{-1}$ (min. = 155 , max. = 1425°s^{-1} , $n = 313$).

I measured the paths of ten different 2.5 M foragers during 24 trips back to the nest. The average path length was 17.09 ± 8.90 cm (max. = 40.06 cm, min. = 5.71 cm) and foragers moved at 2.45 ± 0.61 cm s^{-1} (max. = 3.44 cm s^{-1} , min. = 0.64 cm s^{-1}).

Dance turns: difference angles

I will first give the difference angle results. These results separately consider the clockwise and counterclockwise turns of north and south 2.5 M foragers. (1) Foragers did not show any consistent angular orientation with respect to the nest exit in starting their turns (four Raleigh tests, $P \geq 0.15$, mean vector magnitudes ≤ 0.18). (2) However, the distributions of the stop-difference angles (the orientation angles relative to the exit at the end of turns) are all significantly non-random (four tests, $P < 0.001$, magnitudes of the mean vectors ≥ 0.298 , Table 1). (3) Furthermore, foragers were pointed, on average, at the nest exit. The mean vectors of the stop-difference distributions are not significantly different from 0° ($P \geq 0.06$), and a difference angle of 0° indicates that the forager was pointed directly at the nest exit.

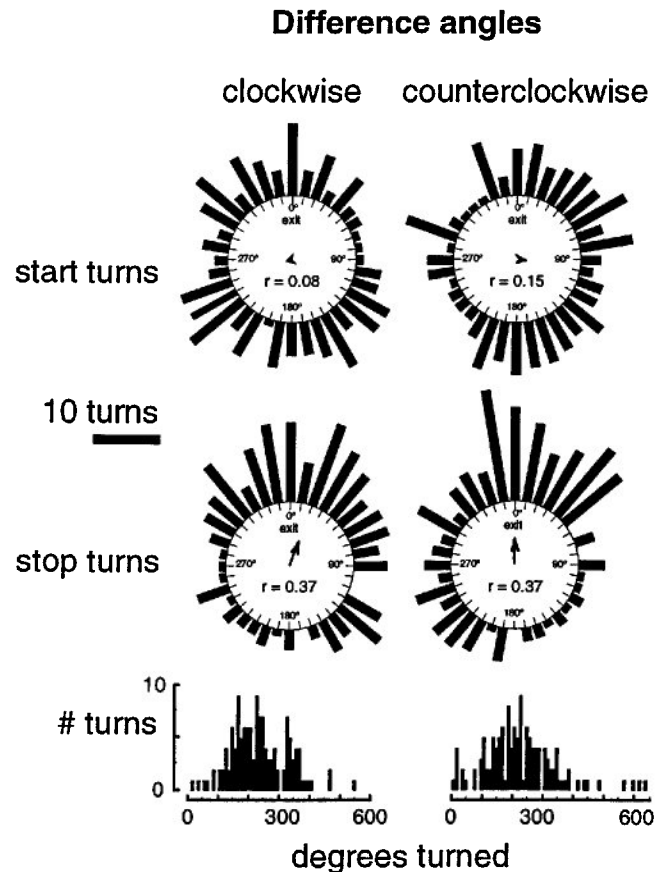


Fig. 8 The distribution of dancer orientations (difference angles) with respect to the nest exit at the start and stop of clockwise turns and counterclockwise turns. Histograms of the number of degrees turned are also shown. The direction and magnitude of the mean vector is indicated with a *scaled arrow* in the center of each circular distribution. The numerical magnitude of each vector is also given. This figure combines the data from north and south dancers feeding on a 2.5 M sucrose solution

Figure 8 pools the data for north and south 2.5 M foragers because I found no significant difference between the start- and stop-difference angle distributions of clockwise and counterclockwise turns performed by these foragers (start-difference angles: four tests, $P \geq 0.110$; stop-difference angles: four tests, $P \geq 0.709$). Thus north foragers and south foragers *started* their clockwise and counterclockwise turns at random orientations with respect to the nest exit, but *stopped* their clockwise and counterclockwise turns, on average, facing the nest exit. The pooled distribution of all stop-difference angles has a mean vector of 8° and is not significantly different from 0° (Table 1, $P > 0.120$).

Dance turns: body angles

The data on forager body angles yields the same results. (1) North 2.5 M foragers and south 2.5 M foragers *started* their clockwise and counterclockwise turns with their bodies at random orientations with respect to

gravity (four tests, $P \geq 0.05$, mean vector magnitudes ≤ 0.10). However, they tended to stop by facing directly upwards (0° with respect to gravity). (2) The distributions of stop body angles for the clockwise and counterclockwise turns of north and south foragers are all significantly non-random (four Raleigh tests, $P \leq 0.005$, mean vector magnitudes ≥ 0.25) and (3) are not significantly different from 0° (four tests, $P \geq 0.09$). Thus, on average, foragers ended their clockwise and counterclockwise turns *with their bodies oriented directly upwards with respect to gravity*. Since a forager can only have a difference angle of 0° and a body angle of 0° when she is positioned along the nest midline (Fig. 1), these data indicate that foragers tended to finish their turns along the nest midline.

Effect of lower-quality food on dance turns

Foragers dancing for a low-quality food source (1.0 M) did not execute their turns as tightly or as rapidly as foragers for a high-quality food source (2.5 M). I compared the behavior of two foragers (55-White and 75-White) as they each alternately foraged at 2.5 M and 1.0 M. For each bee, data were collected during ten performances inside the nest at each sucrose concentration (total of 40 trips from both foragers at both concentrations). Data for clockwise and counterclockwise turns were combined since the previous analysis showed no significant effect of turn direction. Because the body angle data for these foragers was also not significantly different from the difference angle data, I will present only the difference angle data.

At 1.0 M, the distributions of initial unloading difference angles ($Z = 1.55$, $n = 10$, $P > 0.10$), start difference angles ($Z = 0.182$, $n = 25$, $P > 0.10$), and stop difference angles ($Z = 2.75$, $n = 25$, $P > 0.05$) were not significantly different from a random distribution.

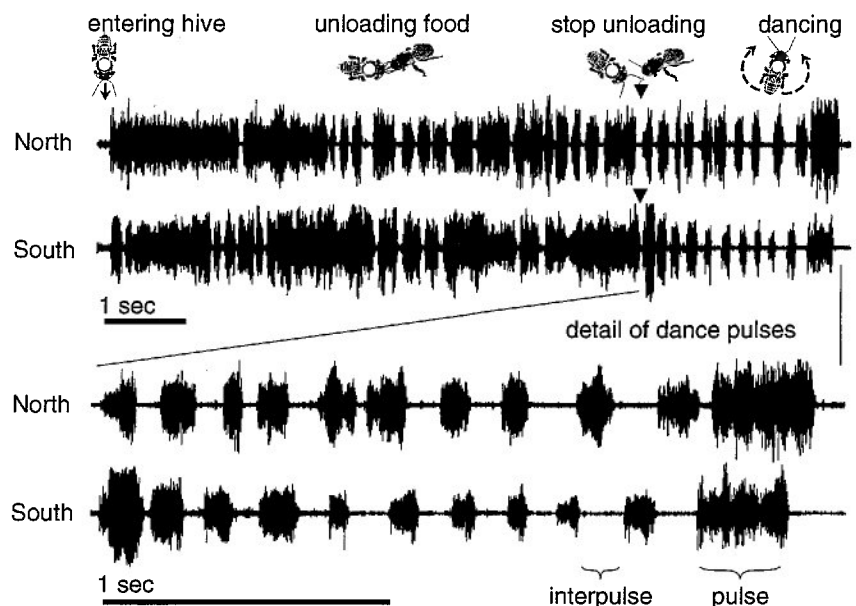
When these same bees foraged at a 2.5 M sucrose solution, they oriented away from the exit while unloading their food ($Z = 34.04$, $n = 124$, $P < 0.0001$) with a mean unloading angle of 171° (not significantly different from 180° , $P > 0.10$). The distribution of start angles for 2.5 M was not significantly different from a uniform circular distribution ($Z = 0.387$, $n = 25$, $P > 0.10$). However, the distribution of stop angles was significantly non-random ($Z = 3.59$, $n = 25$, $P < 0.05$) with a mean stop angle of 0° (not significantly different from 0° , $P > 0.90$). These results accord with the previous data obtained from a larger group of 2.5 M foragers. Thus the distributions of unloading angles and stop angles were random when foragers fed at a 1.0 M sucrose solution, but were non-random when they fed at a 2.5 M sucrose solution.

On average, 1.0 M foragers took 52% longer to make a turn (0.95 ± 0.38 s/turn) than 2.5 M foragers (0.63 ± 0.25 s/turn). This difference is significant ($M_{25,26} = 824$, $P = 0.001$). However, 1.0 M foragers and 2.5 M foragers turned the same average number of degrees ($220 \pm 89^\circ$ at 1.0 M and $221 \pm 90^\circ$ at 2.5 M; $M_{25,26} = 652$, $P = 0.98$). Thus the angular velocity of foragers significantly decreased after they fed at the 1.0 M sucrose solution ($241.5 \pm 66.3^\circ \text{ s}^{-1}$ at 1.0 M, $380 \pm 145^\circ \text{ s}^{-1}$ at 2.5 M; $M_{25,26} = 433$, $P < 0.001$).

Dance sounds

A recruiting forager generally produced pulsed sounds from the time that she entered the nest until the time that she left (Fig. 9). While producing these sounds, her folded wings vibrated dorsoventrally over her abdomen. Figure 9 shows how these sounds corresponded with the different phases of dancer activity. I define a sound pulse as a continuous burst of sound that begins when the forager produces sound and ends when she pauses and

Fig. 9 Waveforms of sounds produced inside the nest by forager 95-Blue (north feeder) and forager 55-White (south feeder). Both feeders were 175 m from the nest. The figures above the waveforms illustrate the corresponding forager behaviors. These waveforms represent the complete sequence of sounds produced by each forager during their respective visits to the nest. The dance pulses are enlarged and the terms *pulse* and *interpulse* are illustrated at the bottom of this enlargement. No amplitude scale is given because the actual amplitude of these sounds could not be determined with the recording setup (see Methods)



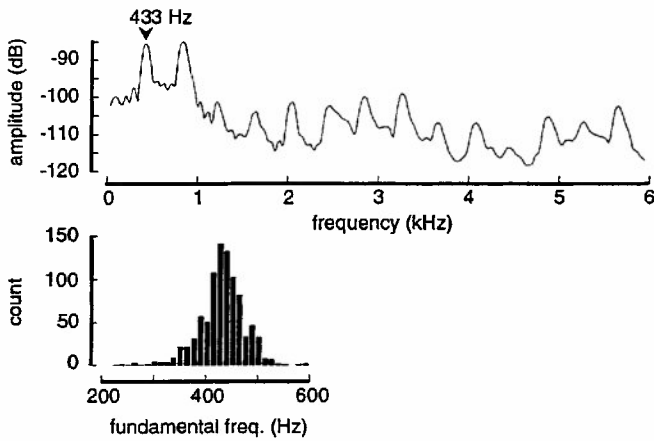


Fig. 10 Frequencies of sounds produced by recruiting foragers inside the nest. The FFT spectrum shows the fundamental frequency (arrowhead) and harmonics obtained from averaging 943 complete sound performances (pooled unloading sound and dance sound data). The histogram gives the distribution of fundamental frequencies from these 943 complete performances

produces no sound. A sound interpulse is the duration of time between pulses when no sound is heard (Fig. 9). In the two cases shown, the foragers produced long pulses interspersed with shorter pulses while unloading food (Fig. 9). After they stopped unloading and while they were dancing, they generally produced a series of short pulses followed by a long pulse.

The sounds produced during unloading have a fundamental frequency of 433 ± 47 Hz, and at least 14 normally detectable harmonics (Fig. 10). Table 2 summarizes data obtained from north and south foragers gathering 2.5 M sucrose solution 175 m from the nest. The data were pooled because no differences were found when the sound data from north and south foragers were compared separately. The unloading pulses (0.29 ± 0.66 s) were longer than the dance pulses (0.13 ± 0.13 s). However, unloading pulse and dance pulse durations were highly variable. The interpulse in-

Table 2 Duration of sound pulses and interpulses produced by bees recruiting for 2.5 M food sources 175 m from the hive (north and south data combined). The mean, median, standard deviation (SD), distribution minimum (Min.) and maximum (Max.), and the total number of sound pulses and interpulses (n) are given for both phases of the forager's performance. The final silent period began when the bee stopped producing sounds and ended when she left the nest. These data were obtained from measurements of 123 complete performances by nine foragers

	Pulses (s)		Interpulses (s)		Final silent period (s)
	Unloading	Dancing	Unloading	Dancing	
Mean	0.294	0.129	0.128	0.261	2.833
Median	0.118	0.080	0.087	0.138	2.454
SD	0.660	0.129	0.195	0.357	3.046
Min.	0.015	0.017	0.003	0.002	0.172
Max.	13.130	1.250	4.938	3.282	23.368
n	3438	818	3430	741	78

tervals were similarly variable. On average, recruiters stopped producing sounds 2.8 ± 3.0 s before leaving the nest.

Antennal positions of followers

Honey bees can detect near-field sounds through the Johnston's organs in their antennae (Kirchner 1994), and I observed followers holding their antennae close to the vibrating wings of the recruiting forager (Fig. 11). The number of bees unloading both groups of foragers was the same ($P = 0.90$), but 2.5 M foragers attracted twice as many antennae to their abdomens as 1.0 M foragers ($P = 0.003$, Table 3). I monitored 1.0 M and 2.5 M foragers for the same total and average periods of time (no significant difference between the distributions of monitoring times: $P = 0.674$, Table 3). Thus 1.0 M and 2.5 M dancers were exposed to the same group of potential followers (they unloaded in the same area for the same amounts of time); however, the abdomens of 1.0 M dancers attracted fewer antennae (Fig. 11).

Table 3 also shows that the distributions of unloading and following bees around the forager were non-random. Unsurprisingly, all unloading bees were positioned around the anterior half of the forager ($P < 0.001$), and significantly more followers were positioned in the posterior half ($P < 0.001$). Overall, the antennae of all bees (unloaders and followers) were evenly distributed around the forager ($P = 0.326$);

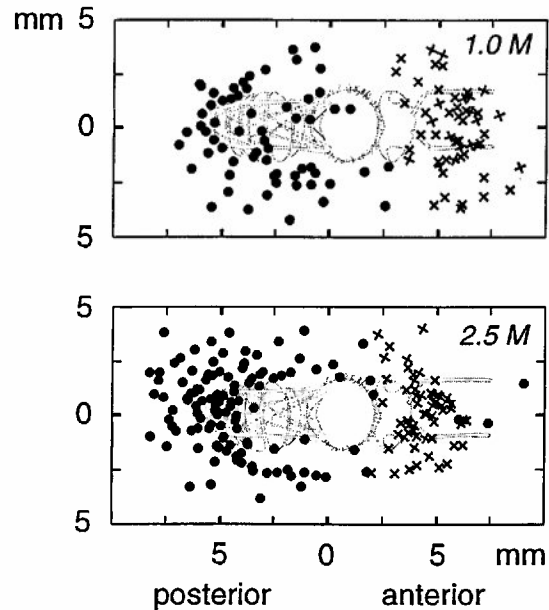


Fig. 11 The positions of 298 antennae around foragers returning to the nest from the south feeder after receiving either 1.0 M or 2.5 M sucrose solution (16 performances from two foragers: eight dances each). Black dots show the antennal tip positions of follower bees. Crosses show the antennal tip positions of food-unloading bees. The zero marks on the scale indicate the longitudinal and transverse body axes

Table 3 Number and distribution of bees attracted to a recruiting forager. Results are given for 16 performances by two foragers (eight dances each). The top half of the table compares the number of unloaders and followers associated with recruiters foraging from either 1.0 M or 2.5 M anise-scented sucrose solutions. Unloaders are bees receiving food, followers are bees that orient towards the

forager. The average duration of the performances (mean \pm 1 SD) is also analyzed. The lower half of the table compares the distributions of bees and antennae around the foragers (pooled data from all 16 performances). The area around the midpoint of each forager was divided into anterior and posterior halves (see Fig. 11) and the presence of antennae in the two regions was recorded

	1.0 M	2.5 M	Chi-square	<i>df</i>	<i>P</i>	
Unloaders (<i>n</i>)	30	29	0.017	1	0.896	
Followers (<i>n</i>)	31	59	8.711	1	0.003	
Seconds/performance	21.8 \pm 3.2	22.6 \pm 3.4	Mann-Whitney test (two-tailed) <i>M</i> = 63.5			0.674
	Anterior	Posterior	Chi-square	<i>df</i>	<i>P</i>	
Unloaders (<i>n</i>)	59	0	59.000	1	\ll 0.001	
Followers (<i>n</i>)	9	81	57.600	1	\ll 0.001	
Follower antennae (<i>n</i>)	19	161	112.022	1	\ll 0.001	
Unloader antennae (<i>n</i>)	118	0	118.000	1	\ll 0.001	
Follower and unloader antennae (<i>n</i>)	137	161	0.967	1	0.326	

however 8.5 times more follower antennae were positioned around the posterior half than around the anterior half of the forager.

Discussion

A recruiting *M. panamica* forager performs a fascinating sequence of behaviors inside the nest. After returning from a good food source, the recruiter enters the nest, searches for a bee to unload her food, unloads her food, dances, and then exits the nest. These actions usually occurred in the area directly next to the exit (Fig. 3A,B) where other inactive foragers were clustered (Fig. 3C). Because previous studies of *Melipona* recruitment have given only a brief description of these behaviors (Lindauer and Kerr 1960), the goal of this paper is to carefully describe the behavior of recruiters inside the nest and thereby provide a foundation for the study of recruitment mechanisms in *M. panamica*.

I divide the behavior of recruiters into two phases, unloading food and dancing. After unloading the majority of her food, a recruiter usually began to make sharp clockwise and counterclockwise turns by pivoting around the approximate center of her longitudinal axis. She moved between turns at a speed of 2.45 ± 0.61 cm s⁻¹ and turned at a rate of $341 \pm 155^\circ$ s⁻¹ (turning $223 \pm 103^\circ$ clockwise or counterclockwise). The direction and order of these turns is random. Foragers produced roughly equal numbers of clockwise and counterclockwise turns, and a goodness-of-fit analysis reveals no significant order to turn direction ($P \geq 0.77$).

In general, 2.5 M foragers faced 192° away from the nest exit as they unloaded their food (mean difference vector). This orientation is not significantly different from 180° (the orientation of foragers entering the nest, $P > 0.085$). These foragers began their turns at random

orientation ($P > 0.05$), but ended their turns facing the nest exit. Their mean stop position vectors are not significantly different from 0° ($P \geq 0.06$, difference angle and body angle data).

Lower-quality food (1.0 M sucrose solution) evidently randomized the unloading orientations and the dance movements. Whereas the 2.5 M unloading orientations were significantly non-random ($P < 0.0001$), 1.0 M unloading orientations of the same foragers were random ($P > 0.10$). Whereas the 2.5 M stop orientations were significantly non-random ($P < 0.05$), the 1.0 M stop orientations of the same foragers were random ($P > 0.05$). Moreover, 1.0 M foragers turned 36% more slowly than 2.5 M foragers ($P < 0.001$), and 1.0 M foragers appeared to produce lower-amplitude sounds, although this was not quantified (see Methods). Fewer foragers were attracted to the abdomens of 1.0 M foragers than to the abdomens of 2.5 M foragers. This was probably not due to a greater concentration of food scent on the abdomens of 2.5 M foragers since both food sources contained equal concentrations of anise scent. Because these results are based upon a relatively small sample size, a more comprehensive study on the effects of changing sucrose concentration is planned.

M. panamica foragers apparently do not encode directional information in their dance movements. (1) North and south foragers were equally likely to make clockwise or counterclockwise turns at any point in their sequence of turns, and I found no significant differences between the turns of north and south foragers ($P \geq 0.15$) with respect to (2) turn direction, (3) angular start position, (4) angular stop position, (5) turn magnitude, and (6) angular velocity. These parameters were chosen because they would also be relevant for dances on the flat surface of the observation nest and on the curved surfaces of natural nests.

Other dance parameters may vary with the direction of the food source; however, direction is apparently not

communicated inside the nest. Removal experiments demonstrate that recruits search in *random directions* when they are separated from experienced foragers as they leave the nest (Nieh, in press). This result is not an artifact of the removal procedure because recruits who have undergone the removal procedure are still able to use distance and height information acquired inside the nest (Nieh and Roubik, in press).

It is important to consider how these data obtained in an observation nest can increase our understanding of behavior in a natural nest. The natural log nest originally built by colony B contained a cerumen and mud funnel leading from the food storage pots to the nest exit. This funnel was initially broad at the food storage pots and narrowed to the width of a single forager at the nest exit. This design is typical of *M. panamica* colonies (D.W. Roubik, personal communication) and I therefore mimicked this structure in the observation nest. The food-unloading platform of the observation nest provides an enlarged version of the natural entrance funnel that leads from the nest exit to the food storage pots (Fig. 1). Moreover, the observation nest did not contain structures that impeded foragers' movements or forager access to different areas of the nest.

In natural nests, I observed foragers dancing within the entrance funnel as well as on the food pots. In the observation nest, almost all foragers danced on the food-unloading platform although they had complete access to the food storage pots. Because the natural entrance funnel is quite narrow and generally crowded with bees moving in and out of the colony, larger groups of follower bees and food-unloading bees congregated on the food storage pots. In the observation nest, many more bees were clustered around the entrance of the unloading platform than were clustered inside the entrance tunnel of a natural nest. Thus access to follower bees and food-unloading bees may be more important than nest structures in determining where foragers will dance.

It should be kept in mind that this paper describes the simplest case of foragers dancing on a relatively flat surface. Foragers in natural nests dance on complex curved substrates (in narrow tunnels or on food storage pots) that greatly influence the running and walking motions of dancers. I have therefore focused on dancer spinning motions since each spin occurred in a relatively small area (Figs. 5, 6) and was thus presumably less affected by surface topography. Likewise, orientation to gravity (body angles) and to the nest exit (difference angles) remain valid measures on a more complex surface. For example, dancers tended to end their spinning movements pointed towards the nest exit, a reference point found in artificial and natural nests (Fig. 8).

Finally, we should consider the function of the movements and sounds produced by recruiting foragers.

The dance movements may generally alert foragers to the presence of food outside the nest and make recruiters more conspicuous to potential recruits. Dancers can

cover large areas with their spinning and running motions, and I have not observed the spinning motions in other contexts. These movements may consequently enable them to reach a wider audience and provide a distinctive signal easily distinguished from other colony activities.

One feature of the dance, the stop orientation of the spins, may reinforce the message that food is outside the nest. Although dancers exhibited no particular orientation at the start of their turns, they displayed a strong tendency to end their turns facing the nest exit. For the last turn in a series, this positions the dancer so that she can rapidly leave the nest. However, it may also emphasize the message that recruits should leave the nest to search for food.

Some evidence suggests that the unloading and dance sounds contain food location information. Esch et al. (1965) reported that *M. quadrifasciata* and *M. seminigra* foragers produced pulsed sounds whose durations were positively correlated with the distance to the food source. *M. panamica* foragers also produced loud pulsed sounds (audible outside the nest) and Nieh and Roubik (in press) report that the duration of sound pulses produced *during the dance phase* is correlated with the *distance* to the food source whereas the duration of sound pulses produced *during the unloading phase* is correlated with the *height* of the food source above ground. This immediately leads to the question of how followers can distinguish between unloading and dance phase sounds.

The dance may enable followers to distinguish between these two phases because a dancer's movements will modulate her dance sounds. Michelsen et al. (1987) showed that the folded, vibrating wings of a dancing honey bee act as a highly directional dipole emitting sounds that are further amplitude-modulated by wagging motions. The directionality of these near-field sounds may provide a conspicuous cue that allows the receiver to detect the orientation and movement of the sender. Honey bee dance followers cluster and orient their antennae around the dancer's abdomen and may use the Johnston's organ located in each antenna to detect these sounds (Towne and Kirchner 1989; Kirchner 1994). *M. panamica* followers also oriented their antennae around the recruiter's abdomen (Fig. 11), potentially allowing them to obtain near-field sound information as well as tactile information from antennal contact with the forager.

Michelsen (in press) has reconsidered the role of near-field sounds in honey bee communication and finds that the amplitude of dance sounds (which must be amplified to be heard) may be too low to be used by follower bees. However, the sounds produced by *M. panamica* foragers can be clearly heard outside an enclosed nest and are thus likely to exceed the minimum detection threshold of the Johnston's organ. Moreover, *M. panamica* recruits may also be sensitive to the vibrations produced by recruiters. Planned studies will examine the sound pressure levels and vibrational displacements produced by recruiting bees.

Future research should focus on determining the characteristics of recruitment behavior that attract followers, the information that followers actually extract from the recruiter, and the mechanisms that followers use to perceive the movements and sounds produced by recruiters. Such studies will not only increase our understanding of *M. panamica's* recruitment system, but will also provide useful comparative data for understanding the evolution of recruitment communication in social bees.

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