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Potential mechanisms for the communication of height and distance by a stingless bee, *Melipona panamica*

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Abstract This study investigates the recruitment communication mechanisms of a stingless bee, *Melipona panamica*, whose foragers can evidently communicate the three-dimensional location of a good food source. To determine if the bees communicate location information inside or outside the nest, we conducted removal experiments by training marked foragers to one of two identical feeders and then separating these experienced foragers from potential recruits as they left the nest. The feeders were positioned to test the communication of each dimension. The results show that recruits do not simply follow experienced foragers to the food source. Height and distance are communicated within the nest, while direction is communicated outside the nest. We then examined the pulsed sounds produced by recruiting foragers. While unloading food, recruiting foragers produced several short pulses and one or more very long pulses. On average, the longest unloading pulse per performance was 31–50% longer ($P \leq 0.018$) for bees foraging on the forest floor than for bees foraging at the top of the forest canopy (40 m high). While dancing, recruiting foragers produced sound pulses whose duration was positively correlated with the distance to the food source ($P < 0.001$). Dancing recruiters also produced several short sound pulses followed by one or more long pulses. The longest dance pulse per performance was 291 ± 194 ms for a feeder 25 m from the nest and 1858 ± 923 ms for a feeder 360 m away from the nest. The mechanism of directional communication remains a mystery. However, the direction removal experiment demonstrates that newcomers cannot use forager-deposited scent marks for long-distance orientation (>100 m from the nest).

Key words Stingless bees · Communication mechanisms · Height communication · Distance communication · Sound pulses

Introduction

The stingless bees (Hymenoptera: Apidae: Meliponinae) exhibit a broad range of foraging strategies with a remarkable diversity of food recruitment mechanisms (Hubbell and Johnson 1978: Roubik 1989). These mechanisms include non-specific excitation with no communication of location, piloting (leading recruits directly to the food source), communication with scent marks deposited to form a scent trail, and communication with sounds produced inside the nest to indicate the distance to the food source (Lindauer and Kerr 1958, 1960; Kerr 1960, 1969; Esch et al. 1965, Esch 1967, review in Nieh and Roubik 1995). Unfortunately, these mechanisms are not well understood and few species have been studied in detail, despite the potential of such information to reveal trends in the evolution of bee recruitment communication. This study therefore focuses on the recruitment communication mechanisms of a stingless bee with good recruitment abilities, *Melipona panamica*.

Initial studies with paired feeder arrays revealed the ability of *M. panamica* to communicate the three-dimensional location of a good food source (Nieh and Roubik 1995). These results initiated the search for communication mechanisms. Lindauer and Kerr (1958) performed water gap experiments and demonstrated that some stingless bees can use scent trails to recruit to a specific three-dimensional location. We repeated these experiments by training *M. panamica* foragers to paired

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feeders placed over a water gap and found that recruits did not need to follow a substrate-deposited scent trail in order to find the correct food source (Nieh and Roubik 1995). Recruits can orient towards a forager-deposited scent beacon at a food source, but can only orient towards this scent beacon within 6–12 m of the food source (Nieh, 1998a). Thus a scent beacon cannot explain the long-distance orientation of recruits.

The pioneering work of Esch et al. (1965) and Esch (1967) suggested that foragers of *M. quadrifasciata* and *M. seminigra* produce sounds inside the nest to communicate the distance to a food source. *M. panamica* foragers also produce an intriguing sequence of movements and sounds inside the nest (Nieh, 1998b). Thus our initial goal was to determine if *M. panamica* foragers communicate location information inside the nest. We therefore conducted removal experiments to determine if height, distance, or direction are communicated inside or outside the nest. Based upon these results, we examined the sounds produced by recruiting foragers and searched for correlations between recruitment sounds and the height and distance to the food source.

Methods

Study site and bee colony

We studied the communication of *M. panamica* foragers in the seasonal tropical moist forest on Barro Colorado Island in Lake Gatun, Panama, from September through November in 1994 and 1995. We conducted these studies during a seasonal dearth of natural food sources that regularly occurs on Barro Colorado Island at the end of the rainy season (Croat 1978). During this period, the availability of natural food sources varied. However at several intervals of 1–2 weeks, bees seldom obtained nectar from natural food sources and seldom performed recruitment sounds or dances for natural food sources (see Nieh 1998b for description of recruitment behavior).

We obtained three wild colonies of *M. panamica* (B, C, and D) from the Santa Rita Ridge region in Colón Province approximately 15 km southwest of Portobello, Panama. Each colony contained approximately 500–600 adults. Nests B, C, and D refer to structures housing colonies B, C, and D, respectively. We transferred colony B into a glass-covered, wooden observation nest to facilitate observations of forager behavior inside the colony (see Nieh and Roubik 1995). We placed nest B inside a laboratory building, inserted the nest entrance through a window, and covered windows around the nest with a velvet curtain and aluminum foil to exclude light. Colonies C and D remained inside their natural log nests.

We placed feeders directly in the forest in all experiments. For the distance and direction experiments, all feeders were placed at sites with comparable altitudes and foliage densities. Because the nests were placed inside a laboratory building, we also chose sites that would require foragers to fly through approximately equal areas of the laboratory clearing.

Feeders

All experiments used identical grooved-plate feeders containing 2.5 M sucrose solution (design in von Frisch 1967). Scented solutions contained 1 μl anise scent (a 27% solution of anise oil in alcohol) per 1 ml of sugar solution. Unscented solutions contained only pure sucrose solution. In experiments with scented feeders, assistants simultaneously dispensed 100 μl of anise scent from calibrated syringes onto each feeder every 60 min (coordinated with two-way radios).

We trained bees by initially placing a feeder (the training feeder) near the nest entrance, waiting for a few foragers to discover it and feed, and then gradually moving the feeder further away in the desired direction (technique described in von Frisch 1967). A control feeder is a feeder at a location to which we did not train bees.

We used powdered paint pigments suspended in shellac to mark all foragers who visited the training feeder during the training procedure and the experiments with a unique combination of colors on the thorax and abdomen (method of von Frisch 1967). For certain observations, we marked bees with numbered tags glued on the thorax (Opalith-Zeichenplättchen). Both marking methods are durable and highly reliable (von Frisch 1967). We censused the number of foragers arriving at the training feeder every 15 min. To control the number of marked foragers, we captured or released additional marked foragers as necessary to maintain a constant number at the training feeder. We captured all bees in Ziploc plastic freezer bags to limit the potential release of alarm pheromone (method discussed in Gould et al. 1970).

The term "recruit" refers to a bee which has found a resource based upon information provided by an experienced forager. Throughout this paper we will employ the term "newcomer" to describe a bee that lands on a feeder and comes from the same colony as experienced foragers, but that was never trained to the feeder. Such a newcomer could have found the feeder either by a random or a directed search.

We marked all experienced foragers, and thus unmarked bees were newcomers. To insure that these unmarked bees came from the same colony as the experienced foragers, we followed three procedures. (1) While training bees to a training feeder, the assistant uniquely marked all newcomers that landed on the training feeder and broadcast these color marks over the radio, enabling us to check at the nest entrance or inside the nest to verify the return of these bees. (2) After a sufficient number of foragers (exact number depending upon the experiment) had been trained, the assistant captured all newcomers as soon as they landed on the training feeder and stored them in plastic bags. At the end of the day, we individually marked and then released all newcomers captured at the *training feeder*. We then checked to see if these newly marked bees returned to the nest. (3) At the end of the day, all bees captured at the *control feeder* were individually marked and placed inside a holding tank provided with honey. Thus they could not return to the colony and communicate the location of the control feeder. Bees could survive in the holding tank for 1–2 weeks. *At the end of the experiment*, when the control feeder was no longer at the location at which these bees were captured, we released all of the bees from the tank and carefully watched for their return to the observation nest. A new and unique set of foragers was trained for each feeder location. Thus bees foraging at any given feeder did not know the location of any other feeder.

Removal experiments: free-foraging phase

To determine if bees communicate location information (direction, height, or distance) inside the nest, we separated experienced foragers from potential newcomers as they left the nest. We placed feeders at two different locations along the appropriate dimensional axis in each experiment. Each morning, we (1) injected 5 ml of 2.5 M anise-scented sucrose solution into the nest entrance to alert experienced foragers of the presence of food at the feeder sites, (2) prepared four feeders, two at each location, (3) filled each feeder with 25 ml of sucrose solution, (4) added 100 μl of anise-scent to the filter paper on top of each feeder, (5) sealed one feeder at each location inside a large Ziploc freezer bag (thus creating the "clean feeders"), (6) set out the other two feeders, one at each location, and (7) allowed foragers to feed ad libitum at the *training* location (the location of the training feeder). This constituted the free-foraging phase. At the *control* location (the location of the control feeder), the assistant captured all bees as soon as they landed. Thus the location of the control feeder could not be communicated. The free-foraging phases enabled us to replicate our 1993 experiments testing the communication of direction, height, and distance with different colonies and served as controls for the removal phases.

Removal experiments: removal phase

After two to three newcomers arrived during the free-foraging phase, assistants at both locations (8) captured any bees remaining on the feeders, (9) removed the feeders, (10) sealed them inside large Ziploc plastic bags, (11) set out the clean feeders, and (12) immediately captured and recorded the arrival times of all bees. We set out clean feeders to eliminate the scent marks deposited by foraging bees. Since no foragers were allowed to feed at the control location, it was not necessary to remove this feeder to eliminate odors deposited by feeding bees. However, the rate of scent evaporation was higher for exposed feeders than for feeders sealed inside plastic bags. To ensure that both control and training locations possessed feeders with equal concentrations of scent, the assistants switched the feeders at both locations. Steps 9–11 were not followed during the direction removal experiments (reasons for this given below).

At the end of the free-foraging phase, we placed a suction apparatus over the nest entrance and removed *all* bees as they flew out of the nest. The suction apparatus consisted of a 29-cm-long clear Lucite tube closed at both ends with corks holding two 2.1-cm (inner diameter) flexible Tygon tubes (6 cm and 15 cm long). We screened the shorter mouthpiece tube with a triple layer of fine mesh to prevent bees and debris from being aspirated into the mouth. We held the longer Tygon tube over the nest entrance.

In a short 2- to 5-min period between the end of the free-foraging phase and the beginning of the removal phase, the experimenter used a suction tube to collect all bees leaving the nest. The experimenter (13) held the tube over the nest entrance and aspirated bees until the tube became full or until no further bees were seen exiting the nest within 5 min, (14) plugged up the nest entrance, (15) emptied the suction tube into large Ziploc plastic bags by blowing through the mouthpiece into a bag held over the suction end, (16) sorted through the collected bees, releasing only the unmarked bees (potential newcomers), (17) stored the remaining bees in the shade, and (18) unplugged the colony and repeated step 13. The experimenter continued this procedure for 20 min (the duration of the removal phase).

The removal phase began as soon as the first unmarked bee was released from a plastic bag. The arrival times of all newcomers were timed relative to this event. However, the beginning of a removal phase was delayed if any assistant detected a forager around the feeder at the end of a free-foraging phase. We waited for the assistant to capture this forager before releasing the unmarked bees.

Because the removal phase prevents experienced foragers from piloting recruits either partially or the entire distance to the food source, recruits are forced to find the food source randomly or based upon information received inside the nest. Recruits could not orient towards other bees on the feeder because assistants immediately captured all bees landing on the feeders during the removal phase. During this phase, assistants also recorded the landing times of all bees. After 20 min, feeder assistants removed the clean feeders, placed them inside their plastic bags, and set out the old free-foraging feeders (in the height and distance removal experiments). The experienced foragers were then released from their plastic bags at the nest. *The free-foraging phase began as soon as the first experienced forager was released.* Once each hour, during a free-foraging phase, assistants simultaneously rescented all four feeders.

Because newcomers may also have oriented to the visual cues provided by other bees on a feeder, we captured but did not count individuals who arrived when other bees were on or around the feeder.

Height removal experiment

We placed nest B on the first floor of a laboratory building 150 m southeast of the canopy tower and trained 20 foragers to the bottom (0 m high) or the top (40 m high) of the tower. We alternately trained foragers to both locations to eliminate the possibility of site bias. The canopy tower is a 40-m-high structure constructed of aluminum sections and sits in an area of forest that is also approximately 40 m high (Nieh and Roubik 1995). During the removal phases, we placed the free-foraging-phase feeders inside sealed plastic bags and set out new feeders at which bees had not fed (steps 9–11). If the height of a food source is communicated inside the nest, then significantly more newcomers should arrive at the training feeder during the free-foraging *and* removal phases. If the height of a food source is communicated outside the nest, then equal numbers of newcomers should arrive at both feeders during the removal phase.

Distance removal experiment

We placed nest B on the second floor of a laboratory building and trained 20 foragers to a feeder 175 m southwest of the nest. We placed an identical control feeder in the same southwest direction, but only 50 m from the nest. During the removal phases, we placed the free-foraging-phase feeders inside sealed plastic bags and set out clean feeders (steps 9–11). If distance information is communicated inside the nest, then significantly more newcomers should arrive at the training feeder during the free-foraging *and* removal phases. If distance information is not communicated inside the nest, then significantly more newcomers should *not* arrive at the training feeder during the removal phase.

Experienced forager and newcomer arrival times

If newcomers simply follow experienced foragers the entire distance to the food source, then newcomers and experienced foragers should arrive at the food source at approximately the same time. To test this hypothesis, we trained one bee (forager 6-yellow) from colony B to a feeder placed 100 m southwest of the nest. A nest observer recorded the times at which this forager entered and exited the nest. Another observer monitored activity at the feeder, immediately captured all newcomers arriving at the feeder, and reported the arrival of newcomers, the arrival of 6-yellow, and the departure of 6-yellow to the nest observer. All data were recorded with a data-logger program running on a Macintosh PowerBook 170.

To analyze these data, we subtracted the arrival times of the experienced forager from the arrival times of newcomers (comparing the arrival times with the smallest absolute differences in order to provide a more stringent test). Because we also recorded the presence of the experienced forager inside the nest, we could identify newcomers that arrived at the feeder while the experienced forager was inside the nest. Throughout this experiment, we allowed only forager 6-yellow to return from the feeder.

Direction experiments

We conducted two direction experiments with colonies B and C in 1995. The first experiment tested the ability of foragers to communicate direction and was designed to replicate our first direction experiment (Nieh and Roubik 1995) with two other colonies in a different season at different field sites. We placed both colonies in the same location, with nest B inside and nest C outside, on the second story of a laboratory building. We trained ten bees from the colony under study to a feeder 175 m either north or south of the nest and placed an identical control feeder 175 m in the opposite direction. Because we used the colonies sequentially, we closed the entrance of colony C while using colony B.

The second experiment tested if foragers could communicate direction inside the nest and tested the importance of locale odors and the scent beacon deposited by experienced foragers. In these direction removal experiments, we placed nest B in the second floor of a laboratory building and trained ten foragers 100 m south of the nest. We placed the control feeder 100 m north of the nest. To test for the importance of the scent beacon and locale odor (odor of the feeder assistant and the surrounding area), we did not use clean feeders during the removal phases. Thus any scent marks deposited by experienced foragers remained on the training feeder.

In the first direction removal trial, we followed the normal removal procedure and confined experienced foragers during the removal phase (steps 16 and 17). In all subsequent trials, we simultaneously released all bees captured in the suction tube by pointing the tube towards the ground and blowing all the bees out. In these cases, recruits could have rejoined experienced foragers after the initial aspiration and received directional information. This procedure tests the importance of the initial link between recruiters and recruits.

Thus if newcomers obtain directional information inside the nest (H1) or if newcomers can orient over long distances to scent marks putatively deposited by an experienced forager (H2), significantly more newcomers should arrive at the training feeder. If neither of these hypotheses is correct, then equal numbers of newcomers should arrive at both feeders.

Observations of behavior inside the nest

We illuminated portions of the unloading platform of observation nest B with a Bausch & Lomb Fiber-lite. 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 (Nieh and Roubik 1995).

We trained bees to 2.5 M anise-scented sucrose feeders located at the same positions used in the height, distance, and direction removal experiments. To compare the behavior of bees feeding at different levels in the canopy tower, we used colony B and trained one group of foragers (bottom foragers) to the base of the canopy tower and one group of foragers (top foragers) to the top of the canopy tower. We allowed only two foragers from each group to forage at any given time and alternately recorded from each group of foragers. This alternation between top and bottom foragers allowed us to control for temporal and environmental changes in behavior that were unrelated to height. We conducted these studies in 1995 and 1996 with the feeders located in the same canopy tower 150 m northwest of the nest.

To compare the sounds produced by foragers trained to different distances, we trained two groups of foragers from colony B to two feeders at increasing distances in the same direction (southwest) from the nest. We compared the following distances: 25 and 420 m, 50 and 360 m, 100 and 360 m, 150 and 360 m, and 250 and 360 m. We allowed only two foragers from each feeder to forage at any given time and alternately recorded from each group of foragers.

We videotaped the sound and motions of bees on the food unloading platform with a Canon L-1 Hi-8 camcorder. To monitor forager sounds, we inserted a Teflon tube (4.5 cm long, 1.7 mm inner diameter) connected to a Radio Shack electret condenser microphone (catalog no. 33-1052) inside the nest, 5 cm from the nest entrance. We passed the microphone output directly to a Canon L-1 Hi-8 video camera with hybrid analog-digital sound recording, manual gain, and VU meter. We calibrated the video camera by directly connecting the 14.2-mV sine wave 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. We then played back the videotape and compared the amplitudes of the recorded sine wave and the original input with a Protek P-2820 20-MHz oscilloscope. We calibrated the Radio Shack microphone by mounting it and a B&K probe microphone (type 4182, with a known frequency response from 20 to 20,000 Hz) 15 cm away from a loudspeaker placed in an anechoic chamber. We then compared the output of both microphones using the Protek oscilloscope. The video camera had a flat frequency response from 75 to 10,000 Hz, and the microphone had a relatively flat frequency response from 50 Hz to 7000 Hz with the exception of two resonance peaks at 750 Hz and 3 kHz (11 dB and 6 dB, respectively, over the average frequency response).

Sound analysis

We digitized dance sounds with a MacRecorder A/D converter (Farallon Computing, Berkeley, Calif), a Macintosh Quadra 800, and the program SoundEdit v1.0 (sampling rate of 22.255 kHz, 8-bits). We analyzed these sounds with the program Canary v1.2.1 (Cornell University, Laboratory of Ornithology). We define a sound pulse as a continuous burst of sound that begins when the forager produces sound and ends when she pauses and produces no sound. A sound interpulse is the duration of time between pulses when no sound is heard. We measured the duration of sound pulses and interpulses from spectrograms. During analysis, we excluded performances with overlapping sounds (approximately 1/4 of all dances recorded). We also did not measure pulses or interpulses obscured by noise. On average, noise obscured less than 4% of pulses and interpulses. We divided the sounds into two categories: sounds produced while the forager was unloading food (food-unloading sounds) and sounds produced while the forager was dancing (dance sounds). The category "dance sounds" includes the short pulses that the forager produces as she stops unloading her food and begins to dance. See Nieh (1998b) for further details on the dance.

Statistics

All averages are presented as the mean ± 1 SD. For experiments involving a comparison of newcomer numbers at the training and control feeders, we assumed that newcomers without location information would be equally likely to arrive at both feeders and used the binomial distribution to calculate *P*-values. For the direction and height experiments, the placement of both feeders at equal distances from the nest generates this expectation. For the distance experiments, the feeder placement leads to the expectation that more newcomers will arrive at the closer feeder if they have no distance information. In this case, our assumption of equal likelihood imposes a more stringent test (Nieh and Roubik 1995). In all cases, we applied one-tailed tests because earlier experiments showed that significantly more newcomers consistently arrived at the training feeder at the correct height, distance, and direction (Nieh and Roubik 1995).

We used two-tailed Mann-Whitney *U*-tests to compare the distributions of sounds produced by bees foraging on the forest floor and bees foraging at the top of the forest canopy (40 m). We used a Kruskal-Wallis test, a non-parametric alternative to ANOVA, to test the relationship between distance to the food source and the duration of sound pulses.

Results

Were any newcomers from other colonies?

By verifying the return of all bees to the observation nest being used, we determined that all of the bees who landed on our feeders were nestmates of the experienced foragers used in each respective experiment. Thus the rate at which wild foragers discovered our feeders was zero.

Do recruiters pilot newcomers?

If newcomers simply follow an experienced forager the *entire* distance to the food source, they should arrive at the same time or shortly after the experienced forager. We conducted timing experiments over 10 days between 10 September and 6 October 1994 and monitored

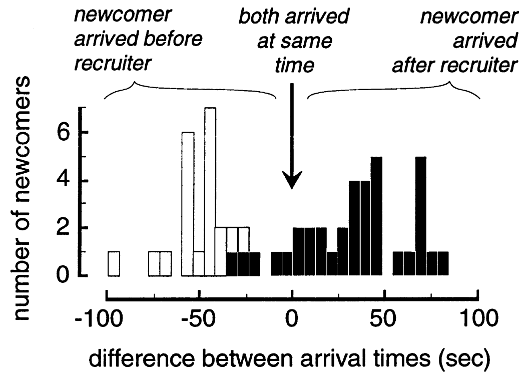


Fig. 1 Distribution of differences between newcomer and experienced-forager arrival times. A negative time difference indicates that the newcomer arrived before the recruiter (the experienced forager). A positive time difference indicates that the newcomer arrived after the recruiter. The time difference equals 0 (*arrow*) when both arrived at the same time. *Open bars* indicate that the newcomer arrived when the experienced forager was still inside the nest (these newcomers were presumably recruited in a previous recruitment bout). *Solid bars* indicate that the newcomer arrived when the experienced forager was outside the nest

84 trips by a single forager (6-yellow) between the nest and the feeder. The recruiter took 31 ± 11 s to fly to the feeder, spent 49 ± 22 s at the feeder, and took 27 ± 10 s to fly back to the nest where she spent 47 ± 17 s. Out of 57 newcomers who arrived during this experiment, 21 (37%) arrived at the feeder while the recruiter was inside the nest (Fig. 1). These 21 newcomers presumably found the feeder based upon information given by the recruiter during a previous recruitment cycle. Interestingly, the arrival time distribution shows only 3 newcomers arriving within 8 s of the experienced forager's arrival (±4 s time difference). The time distribution shows two peaks: newcomers arriving 50 s before the recruiter and newcomers arriving 40 s after the recruiter. These results suggest that newcomers do not simply follow recruiters the entire distance to the food source.

Where and how is height communicated?

In the nine free-foraging trials conducted between 18 October and 30 October 1995, significantly more newcomers always arrived at the training feeder, regardless of its vertical location ($P \leq 0.01$; Fig. 2). These results replicate our previous finding (Nieh and Roubik 1995) that foragers can communicate the height of a good food source.

When we removed bees as they exited the nest and thus prevented recruiters from externally communicating height, significantly more newcomers still arrived at the training feeder, regardless of its location (four trials, $P \leq 0.03$; Fig. 3). In this experiment, we took the precaution of installing clean feeders during the removal phases to avoid scent beacon effects. Thus recruits evidently received height information *inside the nest*. Moreover, the removal procedure evidently did not disrupt the ability of recruits to use this information.

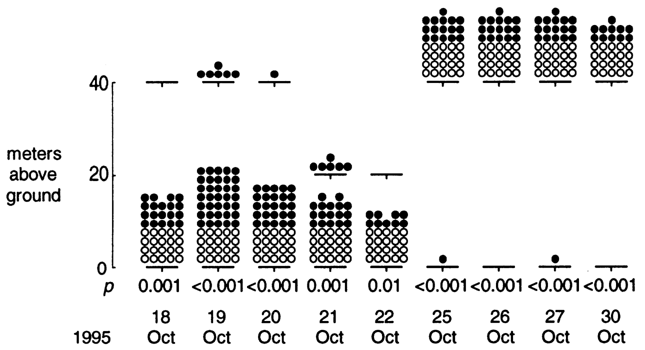


Fig. 2 Results of the height experiment, free-foraging phase. *T icons* indicate feeder positions. *Open circles* represent experienced foragers and thus denote the training feeder. *Solid circles* represent newcomers. Each column represents a different trial and the respective *P*-value and trial date are given below. In all trials, significantly more newcomers arrived at the training feeder

The conspicuous sounds produced by recruiting foragers drew our attention. Figure 4 shows waveforms of these sounds and Table 1 gives a comparison of pulse and interpulse durations for bees foraging at either the bottom (0 m) or top (40 m) of the canopy tower. When *all pulses* are considered, bottom foragers produced pulses that were 9% longer than the pulses of top foragers in 1995 ($P = 0.507$). In 1996, bottom foragers produced pulses that were 52% longer than the pulses of top foragers ($P < 0.001$). In both years, *all interpulses* were shorter for bottom foragers than for top foragers (19% less in 1995, $P < 0.001$; 8% less in 1996, $P = 0.442$).

Bottom foragers and top foragers spent equal amounts of time producing sounds inside the nest in 1995 ($P = 0.308$) and in 1996 ($P = 0.150$; Table 1). However in 1996, top and bottom foragers spent more average time inside the nest (pooled data: 28.5 ± 7.0 s) than top and bottom foragers in 1995 (pooled data:

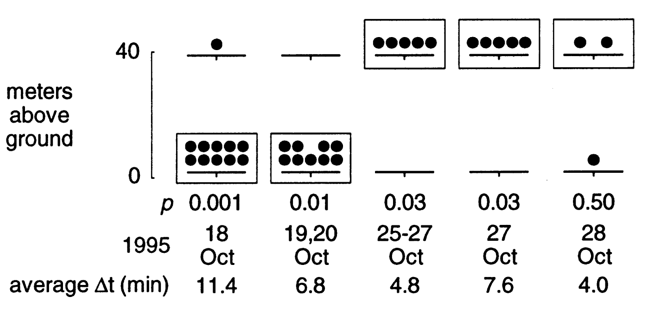


Fig. 3 Results of the height experiment, removal phase. The *solid circles* denote newcomers. *Rectangles* surround the site to which foragers were trained. *T icons* indicate the feeder positions. Each column represents a different trial and the respective *P*-value and trial date(s) are given below. The average time (Δt) between the start of the removal phase and the arrival of each newcomer is also given. Under free-foraging conditions, the average flight time of an experienced forager from the nest to the training feeder was 23 s. In all trials with sufficient data ($n \geq 5$), significantly more recruits arrived at the location of the training feeder ($P \leq 0.03$)

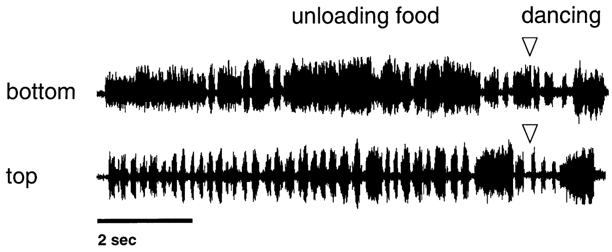


Fig. 4 Waveforms of sounds produced inside the nest by foragers recruiting for feeders in the canopy tower. Forager 75-green fed at the bottom (0 m) and forager 43-blue fed at the top (40 m) of the canopy tower. These data were collected in 1996. An *open triangle* indicates the point at which the forager began dancing. Each sound trace represents one complete performance

18.5 ± 4.7 s). This difference is statistically significant ($P < 0.0001$).

Closer examination of the data reveals an interesting trend. Foragers produced sounds while unloading food and while dancing, but only the sounds produced during food unloading appear markedly different between bottom and top foragers (Fig. 4). The height of the food source does not account for a significant portion of the variation in dance pulse durations ($P = 0.36$). However, the distributions of unloading pulse durations show differences (Table 1). The mean duration of unloading pulses produced by bottom foragers was greater in 1995 than in 1996. The mean duration of unloading pulses produced by top foragers was also greater in 1995 than in 1996. However, within each year, the distribution of unloading sounds produced by *bottom* foragers contains longer pulses than the distribution of unloading sounds produced by *top* foragers (Fig. 5).

One performance is one visit of a recruiting forager inside the nest, and a recruiting forager typically produced a series of short unloading pulses followed by a long unloading pulse during each performance. In 1995, the duration of the average unloading pulse/performance (not including the longest pulse) was 14.7 ± 16.9% of the duration of the longest unloading pulse (LUP) ($n = 2522$, average of 24.7 unloading pulses/performance). In 1996, the same trend occured. The duration of the average unloading pulse/performance (not including the longest pulse) was only 10.9 ± 16.2% of the duration of the longest unloading pulse ($n = 2451$, average of 22.7 unloading pulses/performance). Thus within each unloading episode, a recruiting forager typically produced one long sound pulse and several shorter sound pulses.

Figure 6 is a percentiles plot showing the duration of the LUP for top and bottom foragers in 1995 and 1996. Ranked by percentile distribution within each year, the LUP of bottom foragers is consistently longer than the corresponding LUP of top foragers. In 1995, bottom foragers produced LUPs that averaged 50% longer than the LUPs produced by top foragers ($P = 0.004$; Table 1). In 1996, bottom foragers produced LUPs that

Table 1 Duration of sounds produced by foragers recruiting for food sources at the top (40 m) or bottom (0 m) of the canopy tower. The mean ± 1SD is given along with the results of two-tailed Mann-Whitney *U*-tests comparing the sounds and performance durations of top and bottom foragers. We summarize trends as $b > t$ (mean of bottom sounds > mean of top sounds) or $b < t$ (mean of bottom sounds < mean of top sounds). Data are given for all pulses, all interpulses, and for the longest unloading pulse produced by a recruiter per visit inside the hide. The average duration of performances, the number of performances observed, and the number of individual bees observed is also given

		Mean (ms)	*n*	*P*	
All pulses					
1995	Top	299 ± 571	1,739	0.507	b > t
	Bottom	326 ± 631	2,379		
1996	Top	773 ± 1838	1,155	< 0.001	b > t
	Bottom	1,173 ± 2,778	1,417		
All interpulses					
1995	Top	172 ± 235	1,691	< 0.001	b < t
	Bottom	139 ± 260	2,310		
1996	Top	91 ± 164	1,146	0.442	b < t
	Bottom	84 ± 98	1,399		
Longest unloading pulse per performance (LUP)					
1995	Top	1,936 ± 840	37	0.004	b > t
	Bottom	2,902 ± 1,770	65		
1996	Top	7,802 ± 5,846	52	0.018	b > t
	Bottom	10,245 ± 6,406	67		
		Duration of average performance (s)	Number of performances	*P*	Number of individuals
1995	Top	18.923 ± 3.647	37	0.308	5
	Bottom	18.276 ± 5.201	65		5
1996	Top	28.069 ± 7.047	52	0.150	6
	Bottom	28.888 ± 6.913	67		10

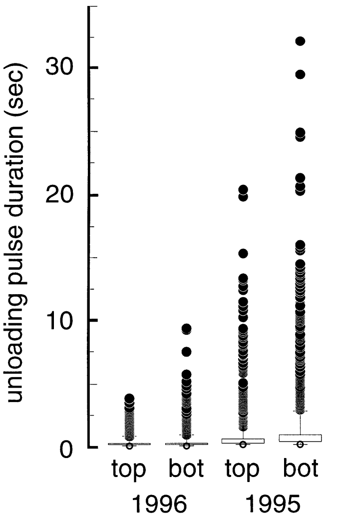


Fig. 5 Boxplots of the duration of all unloading pulses produced by bees foraging at the top or the bottom of the canopy tower. *Solid circles* represent outliers to the main distribution. *Open circles* represent the median of each distribution. The *box* boundaries are set at the first and third quartiles. The *t-bars* indicate the extent of those values that are greater or less than 1.5 times the difference between the first and third quartiles

averaged 31% longer than the LUPs produced by top foragers ($P = 0.018$; Table 1).

Where and how is distance communicated?

In three free-foraging-phase trials, significantly more newcomers arrived at the training feeder, even though an identical control feeder was only 50 m from the nest ($P \leq 0.03$; Fig. 7). This confirms previous results obtained with a different colony (Nieh and Roubik 1995): foragers can communicate the distance to a food source.

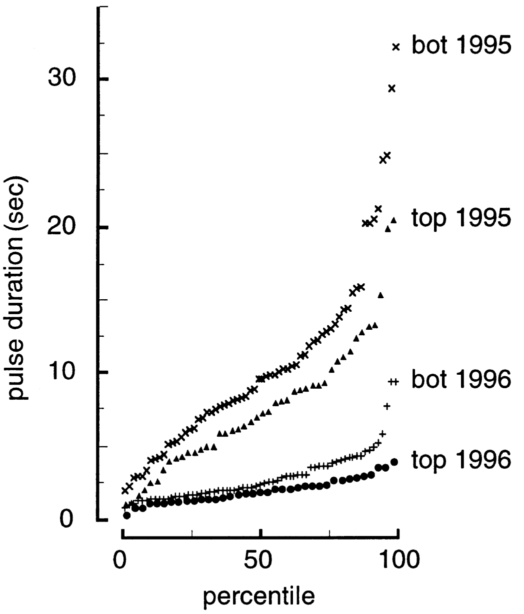


Fig. 6 Percentile plots of the longest unloading pulse/performance by bees foraging at the bottom (*bot*) or top of the canopy tower (*solid circles* unloading sounds produced by top 1996 foragers, *plus signs* bottom 1996 foragers, *triangles* top 1995 foragers, *crosses* bottom 1995 foragers)

Although we prevented recruiters from externally communicating distance in the removal phases by removing bees as they exited the nest and substituting a clean feeder to remove the scent beacon, significantly more newcomers still arrived at the training feeder (three trials, $P \leq 0.05$; Fig. 8). Recruits consequently possessed distance information that they obtained *inside the nest*. Moreover, the removal procedure did not disrupt the ability of recruits to use distance information obtained inside the nest.

Figure 9 shows the waveforms of sounds produced by different foragers recruiting to food sources 50 m, 150 m, and 360 m from the nest. A difference is evident in the dance sounds. Dance pulse duration increases with increasing distance to the food source.

The duration of *all* pulses (unloading phase and dance phase) is positively correlated with distance to the food source ($r^2 = 0.009$, $n = 7748$, $P < 0.0001$). However, distance can only explain 0.9% of the variation in the duration of *all* pulses. Closer examination reveals that the distributions of *all dance* pulses contain increasingly longer pulses as the distance to the food source increases (Fig. 10, Table 2). Distance can explain 4.7% of the variation in the duration of *all dance* pulses ($r^2 = 0.047$, $n = 2978$, $P < 0.0001$).

Analysis of these dance pulses reveals that the best correlation exists between the *longest dance pulse/performance* (LDP) and the distance to the food source (Fig. 11a). Distance can explain 45.5% of the variance in LDPs ($P < 0.0001$). Moreover, distance can explain *96%* of the variance in LDP *average duration* (Fig. 11b; $P < 0.0001$). The average LDP increased by 5 ms/m.

The standard deviations of these LDP distributions are also positively correlated with the distance to the

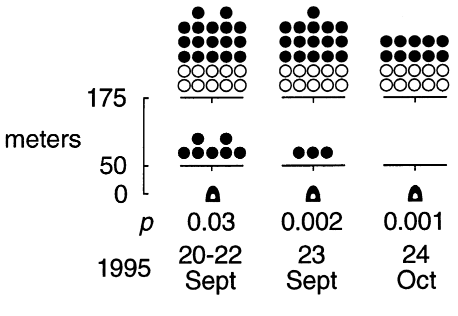


Fig. 7 Results of the distance experiment, free-foraging phase. *Open circles* represent experienced foragers and thus denote the training feeder. *Solid circles* denote newcomers. *Nest* and *T icons* indicate the position of the nest and the feeders, respectively. For each trial, the *P*-value and date are given. In all cases, significantly more newcomers arrived at the training feeder ($P \leq 0.03$)

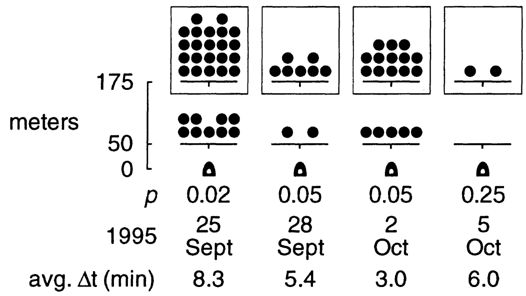


Fig. 8 Results of the distance experiment, removal phase. *Solid circles* denote newcomers. *Rectangles* surround the site to which foragers were trained. *T icons* indicate the feeder positions. Each column represents a different trial and the respective *P*-value and trial date are given below. The average time (Δt) between the start of the removal phase and the arrival of each newcomer is also given. Under free-foraging conditions, the average flight time of an experienced forager from the nest to the 50-m feeder was 9 s (estimated) and from the nest to the 175-m feeder was 31 s. In all trials with sufficient data ($n \geq 9$), significantly more recruits arrived at the location of the training feeder ($P \leq 0.05$)

food source (Fig. 11c, $r^2 = 0.94$, $P < 0.0001$). The standard deviation increased by 2 ms/m.

Interpulse durations remained fairly constant as the distance to the feeder increased. The average duration of *all interpulses* (unloading phase and dance phase) was 0.145 ± 0.238 s ($n = 7563$). The average duration of *dance interpulses* was 0.219 ± 0.358 s ($n = 2767$).

Directional communication

Experienced foragers were able to communicate direction under free-foraging conditions (Fig. 12). Without directional information, newcomers should have arrived in equal numbers at the north and south feeders because both feeders were equidistant from the nest. However in all nine trials, significantly more newcomers from colonies B and C arrived at the feeder visited by experienced foragers, regardless of its location ($P \leq 0.033$). This confirms previous results obtained with a different colony (Nieh and Roubik 1995).

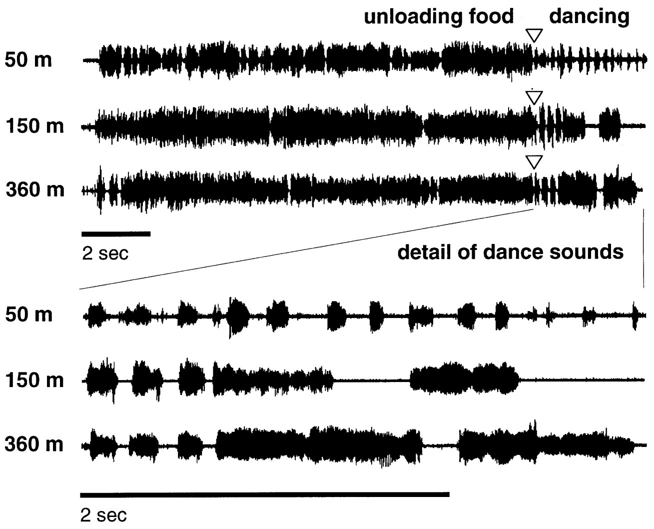


Fig. 9 Waveforms of sounds produced by forager "pink-thorax" during three complete recruitment performances for food sources 50 m, 150 m, and 360 m southwest of the nest. An *open triangle* indicates the point at which the forager began dancing

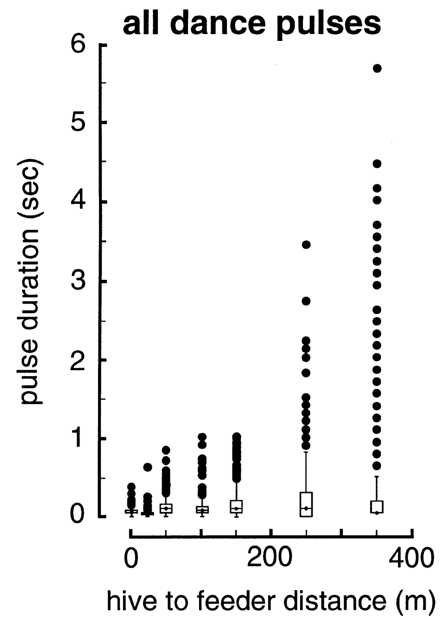


Fig. 10 Boxplots of all dance pulse durations produced by bees for food sources at increasing distances from the nest. *Large solid circles* represent outliers to the main distribution. *Small solid circles* represent the median of each distribution. The *box* boundaries are set at the first and third quartiles. The *t-bars* indicate the extent of those values that are greater or less than 1.5 times the difference between the first and third quartiles

To determine if foragers could communicate direction inside the nest, we retrained bees from colony B to a feeder 100 m south of the nest and placed a control feeder 100 m north of the nest. In all three free-foraging-phase trials, significantly more newcomers arrived at the training feeder ($P \leq 0.011$; Fig. 12). Thus under normal conditions, foragers can communicate the direction of the food source.

However, newcomers evidently received no directional information if they were separated from experienced foragers at the nest entrance. In all five direction removal trials, approximately equal numbers of newcomers arrived at both feeders ($P \geq 0.29$; Fig. 13).

We conducted the first trial with the more stringent procedure of keeping experienced foragers isolated in plastic bags during the removal phases. This prevented experienced foragers from rejoining recruits and giving them directional information after the initial aspiration. However, the next four trials yielded the same results (no communication of direction), although we released potential newcomers and experienced foragers after their initial capture. In these trials, experienced foragers could have rejoined recruits to provide directional guidance, but this evidently did not occur. Thus disrupting the

Table 2 Relationship between pulse duration and distance to the food source. Values are the mean ± 1SD. Three types of data are given: (1) all pulses produced during performance, (2) all pulses produced during the dance phase, and (3) the longest dance pulse in each performance (*n* values in this section also equal the number of performances monitored). Twenty-five different foragers were used to obtain these data

Distance from hive to feeder (m)	All pulses		All dance pulses		Longest dance pulse per performance	
	Mean (ms)	*n*	Mean (ms)	*n*	Mean (ms)	*n*
0	116 ± 103	478	80 ± 56	129	230 ± 74	9
25	96 ± 181	360	67 ± 66	109	291 ± 194	4
50	305 ± 603	1142	136 ± 114	342	395 ± 191	24
100	239 ± 844	1077	125 ± 124	315	419 ± 263	19
150	707 ± 1792	769	211 ± 270	422	978 ± 301	28
250	534 ± 1180	376	357 ±523	178	1599 ± 754	16
360	502 ± 1403	3546	330 ± 551	1483	1858 ± 923	93

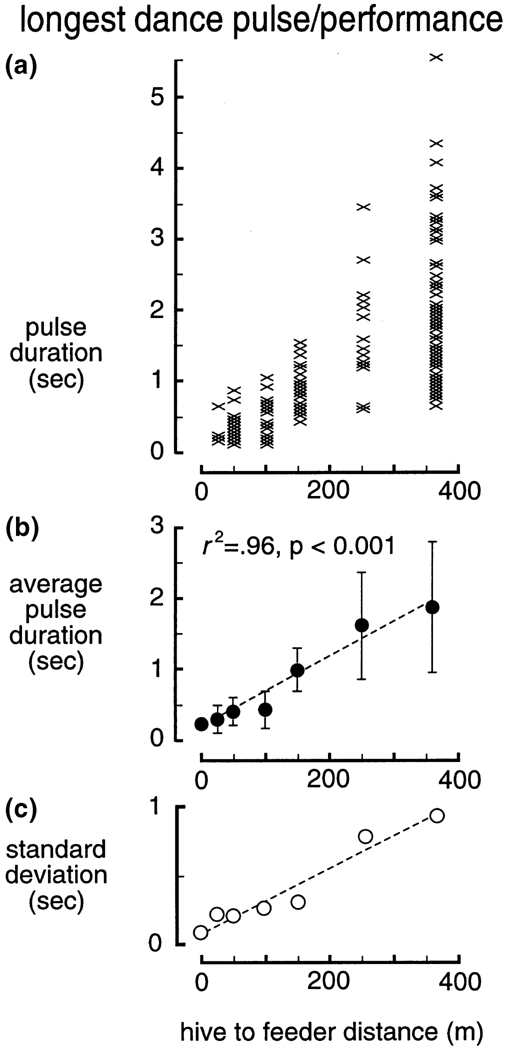


Fig. 11 The relationship between the longest dance pulse/performance and the distance to the food source. **a** Longest dance pulse/performance versus distance. **b** Average and standard deviation of the longest dance pulse/performance at each distance. **c** Plot showing that these standard deviations increased linearly with increasing distance to the food source

initial linkage between recruiter and recruit by aspirating and mixing all bees in a tube was sufficient to prevent the communication of direction. Foragers evidently communicate direction outside the nest.

The direction removal experiment also reveals that newcomers could not orient over long distances (> 100 m) towards the scent beacon or a locale odor. Although the training feeder was not exchanged for a clean feeder and the locale odor was undisturbed, approximately equal numbers of newcomers arrived at the training and control feeder in all trials (Fig. 13).

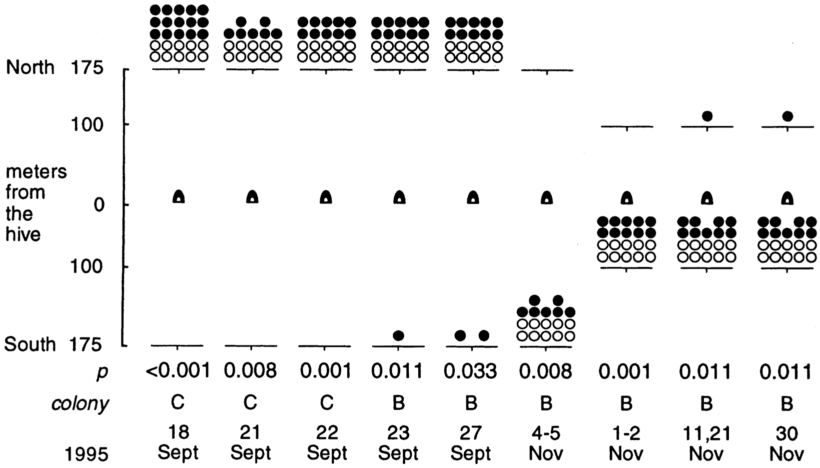
Discussion

Thus *M. panamica* foragers can evidently (1) communicate the direction, height, and distance of a food source from the nest, (2) communicate direction outside the nest, communicate height and distance inside the nest, (3) do not deposit a scent trail for recruits to follow, (4) do not pilot recruits the entire distance to the food source, (5) do not influence the long-distance orientation of recruits with scents deposited at the food source, and (6) produce unloading and dance sound pulses whose durations are related to the height and distance to the food source.

However, given the history of controversy surrounding honey bee communication (Gould 1976), it is essential to consider simple alternative explanations for our results before reviewing the evidence for more complex communication mechanisms.

Could recruits have followed foragers to the food source, but stayed in the vicinity for several minutes without landing? Thus newcomers who followed foragers during each free-foraging phase could have arrived at the feeder at the beginning of each removal phase. Newcomers typically approached the feeder with a circling flight, flew much more slowly than experienced foragers, and emitted a low buzzing tone characteristic of hovering bees. Assistants at the feeders were able to identify the approach of newcomers within at least a 5-m

Fig. 12 Results of the direction experiment, free-foraging phase. *Open circles* represent trained foragers. *Solid circles* represent newcomers. *Nest* and *T icons* indicate the position of the nest and the feeders, respectively. Each column represents a different trial, and the respective *P*-value, colony name, and trial date are given below. In all trials, significantly more newcomers arrived at the training feeder ($P \leq 0.033$)



radius based upon this characteristic flight sound. Moreover, we delayed the beginning of the removal phase if any assistant detected a bee around the feeder at the end of the free-foraging phase. Thus it is unlikely that the newcomers captured during the removal phases were bees that had found the feeder during the previous free-foraging phase but were reluctant to land. In the canopy removal experiments, newcomers arrived at the training feeder 6.72 ± 3.83 min after the beginning of the removal phase. In the distance removal experiments, newcomers arrived at the training feeder 4.39 ± 3.71 min after the beginning of the removal phase. Such a prolonged reluctance to land seems unlikely given that food competition among stingless bees is intense and time critical. The availability of food sources, not nest sites, appears to limit the density of stingless bee species, and the competition for these resources is usually won by the colony that can most rapidly recruit a large number of foragers (Johnson and Hubbell 1974; Hubbell and Johnson 1978).

In the removal experiments testing the communication of distance inside the nest, could more newcomers have arrived at the training feeder because it was located at the same distance as natural food sources? During the removal and free-foraging phases of all trials, we observed no foragers returning to the nest with nectar or pollen from natural food sources for at least 1 week prior to the trials and during the trials. The only foragers who danced or performed recruitment sounds were bees trained to our artificial feeder. Thus attraction to a natural food source located approximately 150 m away from the nest cannot explain the greater numbers of newcomers who arrived at the training feeder during these experiments.

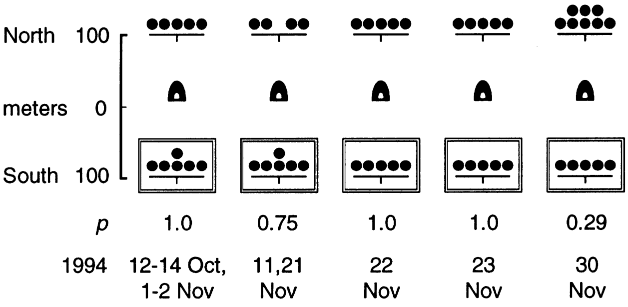


Fig. 13 Results of the distance experiment, removal phase. *Solid circles* denote newcomers. *Double rectangles* surround the training feeder (the site to which foragers were trained) and indicate that the training feeder was not exchanged for a clean feeder during the removal phases. *Nest* and *T icons* indicate the position of the nest and the feeders, respectively. Each column represents a different trial and the respective *P*-value and trial date are given below. In all trials, approximately equal numbers of newcomers ($P \geq 0.29$) arrived at both feeders

Could newcomers have followed a scent trail to the training feeder? Kerr (1994) and Kerr and Rocha (1988) suggested that *M. compressipes* and *M. rufiventris* foragers deposit a scent trail leading from the nest to the food source. However, the direction removal data show that *M. panamica* recruits cannot use a scent trail to find the feeder in the correct direction after being separated from experienced foragers. These results are consistent with an earlier experiment in which newcomers were able to arrive at the correct feeder across a water gap that prevented the deposition of a scent trail (Nieh and Roubik 1995). Thus *M. panamica* recruits do not appear to use scent trails.

Could newcomers have found the training site by orienting towards site-specific odors? Newcomers landed on the "clean" feeder at the training site during the removal phases. They were immediately captured, but they could also have deposited some scent in the few seconds prior to their capture. Moreover, the clean feeder substitution did not eliminate specific locale odors or odors deposited by foragers in the region around the feeder. Could these odors have attracted newcomers to the training feeder? During the removal phases of our direction removal experiments, we did not exchange free-foraging phase feeders for clean feeders. Thirty experienced foragers fed undisturbed at the training feeder and recruited nestmates to this feeder for at least 20 min during each free-foraging phase. If newcomers oriented towards a scent beacon deposited at or near the food source or towards the specific locale odor around the food source, then significantly more newcomers should still have chosen the training feeder during the 20-min removal phases. Yet equal numbers of newcomers arrived at the training and control feeders during the removal phases (Fig. 2). Thus locale odor and forager-deposited scent evidently do not influence the *long-distance* orientation of newcomers. In separate experiments, Nieh (1998a) shows that the forager-deposited scent beacon only influences newcomer choice within 6–12 m of the food source.

Lastly, could recruits have received directional information inside the nest and been disoriented by the removal procedure? Our height and distance removal experiments showed that recruits were still able to find the communicated food source at the correct height and distance from the nest despite the removal manipulation. Thus, in these contexts, our manipulation did not severely disrupt the ability of recruits to find the correct feeder. It is possible that directional information is particularly susceptible to disruption resulting from the removal procedure, and more tests will be required to resolve this issue. However, Nieh (1998b) could not find any correlations between the behavior of recruiting foragers inside the nest and the direction of the food source.

Thus recruits are unlikely to have found the training feeder during the removal experiments by lingering in the vicinity after being guided to the food source during a free-foraging phase or by encountering the training feeder at distances where they habitually foraged for natural food sources. Recruits also did not follow a scent trail or orient over long distances (>100 m) to a scent beacon or locale odor, and thus these explanations also do not account for our height and distance removal results. Finally, the removal manipulation does not appear to inherently cause random search behavior in recruits.

Communication of height and distance

Significantly more newcomers consistently arrived at the locations visited by experienced foragers during the free-foraging and removal phases of our height and distance experiments ($P \leq 0.05$). *M. panamica* foragers therefore appear to communicate two types of information inside the nest: height and distance.

In discussing height communication, we have given the height above ground and compared two heights (the bottom and top of the forest canopy). However, the relevant measure for a forager may be quite different since bee nests are usually located some distance above the ground. Thus from a forager's perspective, the vertical location of a food source with respect to the nest may be most relevant. We also do not know if bees communicate height in a binary fashion (top or bottom) or in a continuous fashion (0–40 m). Because the canopy heights in the typical habitat of this species are fairly low (around 40 m), binary communication may be sufficient, and thus the signal information content could be quite low.

An analysis of the sounds produced by recruiting foragers reveals that within each year, the LDPs of foragers recruiting for a feeder on the forest floor (0 m high) are on average 31–50% longer than the LDPs of foragers recruiting for a feeder at the top of the forest canopy (40 m high; Table 1, Fig. 10). However, LDP durations are highly variable, and the average length of 1995 bottom-forager LDPs is greater than the average length of 1996 bottom-forager LDPs. The same is true for the LDPs produced by top foragers in 1995 and 1996. This variability in LDP duration within each year and between years strongly suggests that other factors are involved in the communication of height, and that we do not have a good understanding of how height is communicated inside the nest. For now, it is interesting to note the consistent LDP differences within each year.

Curiously, the honey bee dance language apparently does not communicate resource height (von Frisch 1967) although honey bees and stingless bees presumably evolved in similar tropical forest environments. Thus the ability of *M. panamica* to communicate food height represents a remarkable and apparently unique feat of communication. The mechanism of height communication requires further careful study, but it should not be surprising to learn that a social bee inhabiting a highly competitive, resource-limited environment where food is dispersed horizontally and *vertically* can communicate the third dimension.

The mechanism for communicating distance seems clearer. Dancing foragers produced longer pulses when recruiting for a more distant food source. When the food source was directly in front of the nest (0 m), these dance pulses were 80 ± 56 ms long. When the food source was 360 m away from the nest, these dance pulses were 330 ± 551 ms long. As the bees began to dance, they produced several short pulses and ended with one or more long pulses. The average duration of the LDP is extremely well correlated with the distance to the food source ($r^2 = 0.96$; Fig. 11).

The importance of the longest unloading pulse and dance pulse per performance and the high variance in unloading and dance pulse durations are puzzling. One major source of variance was our inclusion of strong and weak performances. Recruiters appeared to vary in the strength of their performances and in the number of followers that they attracted. The inclusion of such non-effective or weak performances increased the variance of our data set, and thus a study is planned in which the effectiveness of recruitment performances will be examined by using a colony of marked bees and monitoring which followers from which dance performances actually arrive at the feeder. This should help to identify critical communication parameters, to define what constitutes a "strong" performance, and to determine if recruiters provide other cues to indicate relevant parts of a performance.

It is also possible that sounds alone may not accurately communicate location information. The variance in *Melipona panamica* LDP durations increases linearly with the distance to the food source (Fig. 11), suggesting that the accuracy of distance communication is constant per unit distance. This is surprising given that honeybees increase their accuracy as the distance between the food source and nest increases (and thereby maintain a constant absolute error; Towne and Gould 1988). However, the maximum range of *M. panamica* is approximately 2 km (Roubik and Aluja 1983) and thus additional cues such as orientation to a scent beacon near the food source, orientation to the presence of other bees on the feeder, and partial piloting (see below) may be sufficient to produce the accuracy observed in our early feeder experiments (Nieh and Roubik 1995).

Communication of direction

After we removed all exiting bees and separated experienced foragers from potential newcomers (unmarked bees), newcomers arrived equally at both feeders even though experienced foragers only had knowledge of the south feeder (Fig. 2; $P \geq 0.29$). Prior to the removal manipulation, significantly more newcomers always arrived at the south feeder (Fig. 3; $P \leq 0.03$). Thus newcomers evidently receive directional information outside the nest. However the mechanism for communicating direction remains a mystery. Esch et al. (1965) and Esch (1967) suggested that experienced *M. quadrifasciata* and *M. seminigra* foragers communicate direction with a "zigzag flight" that points towards the food source. We term this "partial piloting" because the recruit is not completely guided to the food source. In several trials, we covered foragers with powdered fluorescent paint pigments to increase their visibility, yet we were unable to see a zigzag flight. Because of the low-light and low-contrast conditions in the forest, we were unable to observe foragers for more than 3–4 m beyond the nest. Thus the "zigzag flight", if it occurs in *M. panamica*, may take place at greater distances from the nest.

Sound perception

The sensory modality through which *M. panamica* foragers perceive sound pulses is not clear. Airborne sounds, vibrations, or both may be involved. Nieh (1998b) reports that dance followers held their antennae close to the vibrating wings of a recruiting forager during the unloading and dance phase of her performance inside the nest. This behavior could allow bees to measure the duration of sound pulses with their antennal Johnston's organs (see discussion in Nieh 1998b).

However, vibrations may also play an important role in *Melipona* recruitment. Lindauer and Kerr (1960) placed two colonies of *M. scutellaris* inside a double nest consisting of a box divided by a wire screen. When a forager of one colony returned from a good food source, she produced buzzing sounds and foragers from *both colonies* appeared at the feeder. The researchers then covered the entrances and floors of both nests with foam rubber. Now when the forager returned and produced buzzing sounds, only foragers from *her colony* appeared at the feeder. After they replaced the foam rubber with galvanized iron, activity in both colonies increased upon the return of a single forager to one colony. They reported: "This led us to conclude that the 'buzzes' are very effective in alerting, and that they are not perceived by any special auditive organ, but (by the legs) as vibrations being transmitted to other bees through the solid parts of the nest. It is of interest that a first attempt to house two colonies of *M. quadrifasciata* in soundproof nests lined with celotex failed, both colonies gradually dying out. It may be that the transmission of vibrations is an essential quality for a Meliponini nest." (Lindauer and Kerr 1960, p. 36).

Recently, Jarau et al. (1998) conducted preliminary studies on recruitment in *M. scutellaris* and *M. quadrifasciata*. They reported that recruiting foragers in both species produced vibrations with frequencies between 300 and 1800 Hz and with prominent peaks at 500, 800, and 1500 Hz.

We are currently characterizing the vibrational transmission characteristics of a natural *M. panamica* nest by using laser vibrometry to make impedance measurements. Our preliminary results reveal that the nest entrance and batumen plates (cerumen and mud structures that wall off the nest cavity) have a vibrational resonance between 400 and 500 Hz. This resonance becomes more pronounced as vibrations propagate over greater distances through these structures. Interestingly, the average fundamental frequency of the airborne sounds produced by recruiting foragers is 433 Hz (Nieh 1998b). The fundamental frequency of vibrations produced by recruiting foragers is likely to be quite similar since vibrations and airborne sounds probably share the same mechanical source, contractions of the flight muscles. Thus *M. panamica* nest structures may be well adapted to transmit vibrations produced by recruiting foragers. Detailed measurements of the vibrations produced by recruiting foragers and the vibrational characteristics of the nest are planned in preparation for future playback experiments that will test the communication of height and distance inside the nest.

Evolutionary implications

Because the communication systems of relatively few stingless bees have been characterized and the phylogeny of the Meliponini (stingless bees) is largely unresolved (Michener and Sakagami 1990), we cannot yet address the fascinating question of how stingless bee recruitment systems evolved. However, the honey bee communication system is well characterized and thus we can compare the complex recruitment systems of two highly social bees. Stingless bees and honey bees (Apini) may be closely related, and stingless bee recruitment systems were consequently seen as a potential model for the evolution of the honey bee recruitment system (Esch et al. 1965). Unfortunately, current opinion is divided on the evolutionary relationship between these two groups. Molecular data suggest that the Meliponini are most closely related to the Bombini (bumble bees) whereas morphological data suggests that the Meliponini are most closely related to the Apini (Chavarria and Carpenter 1994, Koulianos et al., in press). The Bombini are not highly social and do not appear to recruit for food sources (Michener 1974). Thus the communication systems of *Melipona* and *Apis*, although sharing the use of sounds, may have evolved independently. Nonetheless, it is interesting to note that both systems use complex communication mechanisms while retaining relatively simple mechanisms: scent marking to guide orientation near the food source (Nieh 1998a) and non-directional alerting dances inside the nest (the round dance in *Apis mellifera*; von Frisch 1967). Thus simple and complex recruitment mechanisms coexist in species with advanced communication systems. Since information is not always perfectly transmitted or received in any single channel, the vital task of foraging may be better served by a redundancy of multiple communication channels.

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