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*Original article*

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**The role of a scent beacon in the communication of food location by the stingless bee, *Melipona panamica***

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**Abstract** *Melipona panamica* foragers can deposit a scent beacon that influences the orientation of foragers near a food source. In misdirection experiments, newcomers (bees from the same colony as trained foragers) consistently preferred the feeder at which trained foragers had fed (training feeder) over an identical feeder at which bees had never fed (control feeder) even when the training feeder was placed at a site where experienced foragers had never foraged. Through similar misdirection experiments, the effective radius of the scent beacon was determined to be greater than 6 and less than 12 m. Foragers may deposit this beacon during a sequence of departure behaviors performed at the feeder. Prior to leaving the feeder with a load of sugar solution, bees tended to perform the following sequence of behaviors: (1) spinning, (2) grooming, (3) abdomen dragging, (4) excreting anal droplets, and (5) producing sounds, although not all behaviors were performed prior to each departure or at all sucrose concentrations (0.5–2.5 M). As sucrose concentration increased, the number of newcomers significantly increased, and the number of experienced foragers producing sounds and spinning on the feeder increased. The exact source of the scent beacon remains a mystery. However, three important sources have been excluded. When choosing between identical paired feeders, foragers were not attracted to the feeders with (1) anal droplets, (2) extracts of sucrose solution at which foragers had fed, or (3) mandibular gland extracts. They were indifferent to the first two preparations and exhibited only typical alarm behavior towards the mandibular gland (MG) extract: they oriented towards the feeder with MG extract but consistently landed on the feeder with no MG extract. Other authors have suggested that *Melipona* foragers deposit

anal droplets to attract recruits, however the frequency of anal droplet production and the mass of anal droplets produced by *M. panamica* foragers are negatively correlated with sucrose concentration. Thus the scent beacon is evidently not deposited with anal droplets, infused into the feeder solution, or produced by mandibular glands.

**Key words** Stingless bee · Communication · Pheromone · Scent beacon · recruitment

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**Introduction**

Nieh and Roubik (1995) conducted paired feeder experiments to test the communication of food location by *Melipona panamica* and demonstrated that foragers can communicate the distance, direction, and height of a good food source. Through water gap experiments, they demonstrated that this communication system does not rely upon a scent trail (Nieh and Roubik 1995). Subsequent experiments have revealed that experienced foragers communicate direction outside the hive and height and distance inside the hive (Nieh 1997). To test the communication of direction outside the hive, all bees were removed as they left the hive and then unmarked bees (potential newcomers) were released while marked bees (experienced foragers) were retained. All bees visiting the feeder had been previously marked. After this manipulation, equal numbers of newcomers arrived at two feeders located 100 m from the hive but in opposite directions. Thus directional information was not transferred or consolidated when newcomers were separated from experienced foragers outside the hive. Similar forager-removal experiments demonstrated that distance and height are communicated inside the hive. In these experiments, significantly more newcomers arrived at the training feeder than at the control feeder after undergoing the removal procedure (Nieh 1997). The distance and height information may be acoustically

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communicated by dancing foragers inside the hive (Nieh 1997).

Because pheromones play an important role in foraging systems of stingless bees (Lindauer and Kerr 1958, 1960; Roubik 1992), their potential role in the recruitment of *M. panamica* foragers must also be considered. The best documented pheromone mechanism is the scent trail deposited by *Scaptotrigona postica* to guide newcomers to a food source (Lindauer and Kerr 1958, 1960; Kerr et al. 1963). Does *Melipona* use a similar mechanism? Kerr (1994) and Kerr and Rocha (1988) proposed that *M. rufiventris* and *M. compressipes* foragers deposit a scent trail leading from the hive to the food source. They observed successful foragers landing upon a leaf or blade of grass near the feeder, grooming, and then rubbing their mandibles against the substrate. Recently, Aguilar and Sommeijer (1996) have also suggested that *M. favosa* foragers deposit scent marks in the form of anal droplets to help communicate a feeder's location.

The goal of my study was to establish the role of scent marks deposited outside the hive in the communication of food location by *M. panamica* foragers. The following questions were investigated:

1. Is there a scent beacon?
2. What is the effective radius of the scent beacon?
3. How is the scent beacon deposited?
4. What is the source of the scent beacon?

To address these questions, (1) newcomers were misdirected with the putative scent beacon; (2) paired feeders were used to determine the maximum distance at which a scent beacon could influence newcomer choice; (3) correlations between the behavior of foragers at the feeder and the quality of the food source (sucrose concentration) were examined; and (4) feeders baited with anal droplets, concentrated sucrose solution at which foragers had fed, and mandibular gland extracts were used in an attempt to identify the source of the scent beacon.

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## Methods

### Study site and bee colony

The study was conducted in the seasonal tropical moist forest on Barro Colorado Island in Lake Gatun, Panama from September to November in 1992, 1994, and 1996. Two colonies (A and B) of *M. panamica* (Hymenoptera: Apidae: Meliponinae) were obtained from the Santa Rita Ridge region in Colón Province approximately 15 km southwest of Portobello, Panama. Each colony contained approximately 500–600 adults. Both colonies were transferred into glass-covered, wooden observation hives (Nieh and Roubik 1995). In all experiments, each hive was placed inside a laboratory building, and the hive entrance was inserted through the window. To reduce the disturbing effects of light, I enclosed the area around the hive with a velvet curtain and covered the laboratory windows with aluminum foil (Nieh and Roubik 1995). Colony A was used in 1992. Colony B was used in 1994 and 1996.

### Feeders

I used identical grooved-plate sucrose-solution feeders in all experiments (von Frisch 1967; Nieh and Roubik 1995). The sucrose concentrations of these solutions ranged from 0.5 M to 2.75 M. All scented solutions contained 1  $\mu$ l anise scent/ml sucrose solution. In all experiments with scented feeders, assistants simultaneously dispensed 100  $\mu$ l of anise scent from calibrated syringes onto filter papers placed atop each feeder each 60 min (coordinated with two-way radios).

In certain experiments, I measured wind direction by attaching 4-cm pieces of yarn to the feeder stands. By observing these strings and noting the direction with compasses, assistants recorded wind direction for wind speeds greater than 0.1 m/sec (the lowest wind level that deflected the strings). A digital Turbo Meter (Davis Instruments, Hayward, California) wind speed indicator was used to calibrate the strings' wind sensitivity.

### Training

The training feeder is the feeder used to train bees to a specific foraging location (Nieh and Roubik 1995). It is also the only feeder at which bees are allowed to forage. A control feeder is a feeder to which bees were not trained. Bees were trained by initially placing a feeder near the hive entrance, waiting for a few foragers to discover it and feed, and then gradually moving the feeder farther away in the desired direction (von Frisch 1967).

I used powdered paint pigments suspended in shellac to mark each forager visiting the training feeder with a unique combination of colors on the thorax and abdomen (von Frisch 1967). For certain observations, assistants marked bees with numbered tags glued on the thorax (*Opalith-Zeichenplättchen*). Both marking methods are durable and highly reliable (von Frisch 1967). Assistants censused the number of foragers arriving at the training feeder each 15 min and removed or released marked foragers as necessary to maintain a constant number at this feeder. All bees were captured in Ziploc plastic freezer bags to limit the potential release of alarm pheromone (method discussed in Gould et al. 1970).

A "recruit" is generally understood to be a bee who has found a resource based upon information provided by an experienced forager. However, it is also possible that some bees find the resource through a random search. The distribution of new bees arriving at the control and training feeders will indicate whether communication was involved, but it is not possible to know whether any specific bee coming to the feeder has arrived based upon communicated information or a random search (unless its complete flight path could be observed). To indicate this ambiguity, I will employ the term "newcomer" to describe a bee who lands on a feeder and comes from the same colony as experienced foragers, but that was never trained to the feeder. Such a bee could have found the feeder either by a random or a directed search. Since some experiments eliminated critical information and evidently forced bees to find the feeder by a random search, the term "newcomer" is more accurate than the term "recruit." Because all experienced bees were marked, a newcomer was an unmarked bee.

Only newcomers who came from the colony under study were used as data points. In order to determine which bees visiting the feeders came from the colony under study, three procedures were followed:

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 hive entrance or inside the hive to verify the return of these bees. Any bees not from the colony under observation were immediately captured in plastic bags and sacrificed upon their next return to the feeder (Nieh and Roubik 1995).
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, all newcomers

captured at the training feeder were individually marked and then released. If any of these newcomers did not return to the hive, they were presumed to be from another colony and were immediately captured and sacrificed upon their next visit to the feeder.

- At the end of the day, all bees captured at the control feeder were individually marked and placed inside a glass holding tank provided with honey. Thus they could not return to the colony and communicate the location of the control feeder. They could live in the holding tank for a maximum of 14 days, depending upon the age of the forager at the time of capture. At the end of the experiment, when the control feeder was no longer in the location at which these bees were captured, all the bees were released from the tank and the return of these bees to the observation hive was carefully observed. In order to ensure that the bees did not die before being released, the longest experiment was limited to 9 days. None of the bees captured in this experiment died during this period. Any bees that did not return were presumed to belong to another colony. All data on bees that were not nestmates of the trained foragers were removed from analyses.

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. When switching to a new feeder site, I captured all bees trained to the old site and confined them to the glass holding tank until all experiments were completed (method discussed in Nieh and Roubik 1995).

#### Free-foraging and removal phases

Several experiments employed free-foraging phases and removal phases. During a free-foraging phase, the assistant allowed a fixed number of marked bees to forage ad libitum at the training feeder. As always, the assistant captured and released marked foragers to maintain a constant number of foragers. During the removal phases, I used a tube to aspirate all bees leaving the hive, separated the marked bees (experienced foragers) from the unmarked bees (potential newcomers), and released only the unmarked bees. Any newcomers at the feeder were immediately captured in Ziploc plastic bags before they had a chance to forage. Newcomers who approached while another bee was on or within 5 m of the feeder were captured as soon as they landed, but were not counted. Thus experienced foragers were unable to transmit any directional information to newcomers and were not present on the training feeder when newcomers arrived (Nieh 1997). This enabled newcomers to make a choice between the training and the control feeder based solely upon olfactory differences.

A free-foraging phase typically lasted 30–40 min and terminated after one to three newcomers had arrived at the feeder. A removal phase lasted 20 min. Free-foraging and removal phases alternated so that experienced foragers remained motivated to recruit for the training feeder. At the end of each removal phase, the assistant sprayed the control feeder with a 50% ethanol solution, wiped it clean with a paper towel, and sealed the paper towel inside a Ziploc plastic bag.

#### Determining how foragers deposit the scent beacon

As the concentration of sucrose solution decreased, the rate of recruitment decreased, but the number of experienced foragers visiting the feeder remained constant. I therefore expected foragers to preferentially deposit the scent beacon at higher sucrose concentrations. To determine how the scent beacon was deposited, the sounds and motions of landing, foraging, and departing foragers at different sucrose concentrations were videotaped (filming with a Canon L-1 Hi-8 camcorder). To monitor forager sounds, a Radio Shack electret condenser microphone (cat#33–102) held 5 cm above the feeder was used. The Hi-8 tapes were copied onto VHS tapes and then a JVC BR-S525 U video-cassette player (30 frames/s) was used to analyze forager behavior. I trained foragers to an anise-

scented feeder (100 m south of colony B) filled with anise-scented sucrose solutions ranging in concentration from 0.5 to 2.5 M. Because bees began foraging immediately after landing and did not perform any other behaviors until preparing for departure, the presence and order of five departure behaviors were scored: (1) spinning, (2) grooming, (3) abdomen dragging, (4) excreting anal droplets, and (5) producing sounds. For example, some bees spun, groomed, and produced an anal droplet before flying off. Other bees performed a different set of behaviors in a different sequence. Sequence order was examined with a transition probability matrix.

In 1992, I used colony A to determine whether there was a correlation between sucrose concentration and the production of anal droplets. An anise-scented feeder was placed 8 m away from the hive along a forest corridor, that made it possible to see bees flying to and from the feeder and to observe droplets deposited on foliage or on the feeder.

Because I observed nearly all droplets being deposited within a few meters of the feeder, I repeated this experiment in 1994 with colony B but with the anise-scented feeder placed in the forest 100 m south of the hive. Eppendorf micro-centrifuge tubes containing thin strips of Whatman filter paper were numbered and weighed beforehand with a Mettler AE 163 balance. The assistant placed the feeder on a wax paper disk. To collect a droplet, the assistant took out a pair of tweezers, opened the tube, adsorbed the anal droplet with the filter paper, replaced the filter paper inside the tube, and sealed the tube. The assistant re-weighed these tubes at the end of each day and calculated the weight difference.

#### Searching for the source of the scent beacon

I tested three substances for their ability to attract foragers to the feeder: (1) anal droplets, (2) mandibular gland extracts, and (3) sucrose solution at which foragers had repeatedly fed.

The assistant collected five anal droplets in each tube with the method given above. After collection, the anal droplets were immediately placed inside a freezer. Droplets were collected from foragers foraging at different concentrations of sucrose and from foragers who (1) laid a droplet and then departed or (2) groomed, laid a droplet, and then departed. To prepare blank vials, the assistant opened a sealed tube, removed the filter paper with a clean pair of tweezers, held it away from the feeder for 5 sec (the average amount of time required to collect five anal droplets), replaced the paper inside the tube, and resealed the tube. The assistant made one blank after filling each anal droplet tube. These blanks were also immediately frozen.

To obtain sucrose solution at which foragers had repeatedly fed, 40 foragers were allowed to forage ad libitum for 30 min from a feeder initially filled with 20 ml of 2.5 M unscented sucrose solution (with no scent paper). At the end of this interval, the remaining sucrose solution was thoroughly mixed (5 ml) and 1 ml/tube was dispensed into clean micro-centrifuge tubes. For the blanks, 1 ml/tube of fresh unscented 2.5 M sucrose solution was dispensed into other tubes. All tubes went then frozen.

To obtain mandibular gland extract, a net was placed outside the nest entrance, and five foragers were captured as they departed the hive, killed by coding in a refrigerator. One mandibular gland was dissected out from each forager. I placed five glands in a micro-centrifuge tube with 1 ml of acetone, vortexed the sealed tube for 2 min, and then pipetted out the extract into clean micro-centrifuge tubes. Three dilutions were made from this extract: 1/1 (200  $\mu$ l of extract), 1/20 (10  $\mu$ l of extract in 190  $\mu$ l of acetone), and 1/40 (5  $\mu$ l of extract in 195  $\mu$ l of acetone).

Attraction experiments were conducted with experienced foragers trained to a feeder 100 m south of colony B. The assistant placed two clean feeders 0.5 m away on opposite sides (east and west) of the training feeder. These clean feeders were covered during each 20-min free-foraging phase. Ten minutes before the end of the free-foraging phase, the assistant began capturing all foragers and I brought out and thawed the frozen vials. The assistant then uncovered the clean feeders, and taped two vials on opposite sides of each clean glass feeder dish. One feeder was

designated the “baited” feeder and held the substance of interest. The opposite feeder was designated the “blank” feeder and held blank vials.

To begin the attraction trial, the assistant sealed the training feeder inside a plastic container (but did not change its position), and opened the micro-centrifuge tubes at the baited and the blank feeder (always opening the blank tubes first). During these experiments, the assistant sat facing north (facing the direction of incoming foragers) 0.5 m south of the training feeder and placed equipment and plastic bags containing captured bees inside a sealed plastic garbage bag directly behind herself. A second assistant sat opposite, facing south and also 0.5 m from the training feeder. The assistants consequently formed a north-south axis and the clean feeders formed an east-west axis with both axes centered on the training feeder. The north-facing assistant released one bee at a time. Each 10 min, the south-facing assistant recorded (1) the number of approaches that the bee made to each feeder (number of times the bee came within 5 cm of a feeder) and (2) the feeder upon which the bee finally landed. The South-facing assistant recaptured the forager as soon as it landed.

### Statistics

In the initial experiments comparing the number of newcomers arriving at each of two paired feeders, the two-tailed binomial probability was calculated based upon the assumption that bees had an equal likelihood of arriving at both feeders ( $P = 0.5$ ). Because significantly more newcomers always landed on the training feeder in these initial experiments, the one-tailed binomial probability was used in the subsequent effective-radius experiment. (This experiment was conducted last, after the vial attraction experiments.) To compare two distributions, the Mann-Whitney  $U$ -test (test statistic =  $M$ ) or a sign test was used. Averages are presented as mean  $\pm$  1 SD.

### Other methods

Several experiments used highly specific methods. To facilitate interpretation of these results, These methods are described before the corresponding results in the Results section.

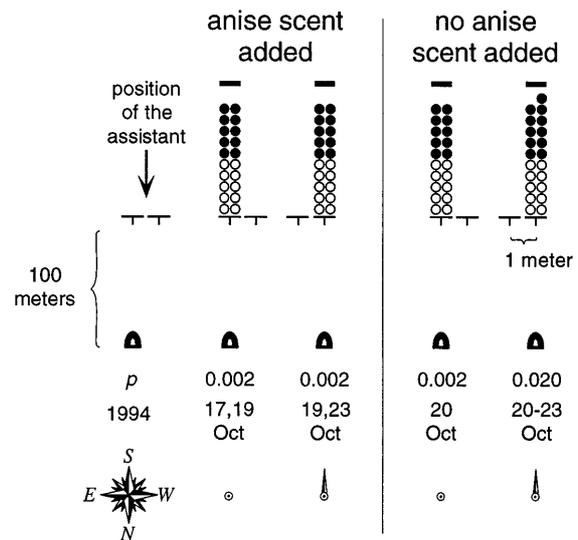
## Results

### Foragers from other colonies

By verifying the return of all newcomers to the observation hive, all bees that landed at the feeders were confirmed as both nestmates of the experienced foragers used in the each respective experiment. Thus no foragers from other colonies discovered the feeders at any point during these experiments.

### Initial evidence for a scent beacon

To determine whether experienced foragers deposit an attractive scent at the feeder, I placed a second feeder only 1 m away from the original training feeder (Fig. 1). If foragers deposit an attractive scent, newcomers were expected to land preferentially on the training feeder. In 1994, ten foragers were trained to a 2.5 m sucrose solution feeder located 100 m south of colony B. An identical control feeder was placed 1 m to the east or west

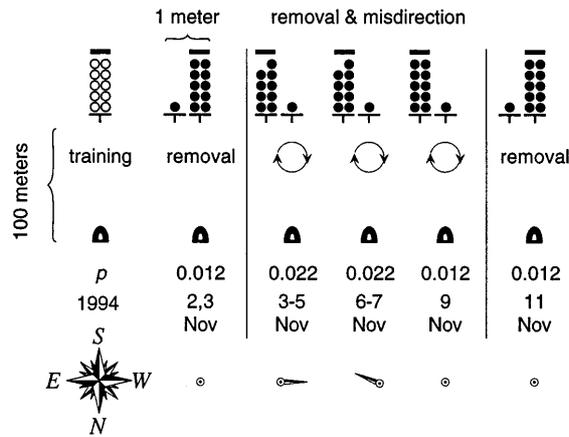


**Fig. 1** Is there evidence for a scent beacon? The position of the assistant relative to both feeders is shown by the arrow on the left. Experienced foragers are represented by *open circles* and newcomers by *filled circles*. The training feeder is marked with a *solid bar*. The positions of the training feeder and the control feeder were alternated to eliminate the possibility of site bias. The feeders were placed 100 m south of the hive (*solid hive symbol*). Vertical and horizontal dimensions are not shown to the same scale. In the two trials with anise scent, both feeders were equally scented. The *compass rose* gives the cardinal directions. For each trial, *pointers* indicate wind direction. A *dot within a circle* indicates no wind. The binomial probability and date of each trial are also given

side, alternately, of the training feeder (to control for site bias), and an assistant scored the number of newcomers landing on each feeder. To avoid blocking incoming bees and biasing newcomer choice, the assistant sat behind and equidistant from both feeders and faced the forager arrival direction (Fig. 1). In the first two trials, the assistant filled the feeders with anise-scented sucrose solution and added anise scent to the filter papers on top of each feeder. In the second two trials, unscented sucrose solution was used at both feeders, and scent was not added on top of the feeders.

Regardless of whether both feeders were anise-scented or unscented, all experienced foragers and newcomers landed on the training feeder ( $P \leq 0.02$ , Fig. 1), even when both feeders were only 1 m apart. Placement of the control feeder to the left or the right of the training feeder had no effect; bees always landed at the training feeder (Fig. 1). Thus site bias did not explain these results. Three explanations remained: (H1) newcomers are only attracted by the presence of other foragers on the training feeder, (H2) newcomers have an extremely precise knowledge of the location of the food source (azimuthal accuracy of at least  $0.56^\circ$  at 100 m), or (H3) newcomers are attracted to a scent beacon deposited by experienced foragers on the training feeder.

In the previous experiment, newcomers could have oriented towards the foragers on the training feeder (H1). To eliminate this possibility, an experiment was



**Fig. 2** Could recruits be misdirected to visit a location where experienced foragers never foraged? Open circles denote experienced foragers and filled circles denote newcomers. A solid bar marks the training feeder. In the training phase, 10 foragers were trained to a feeder 100 m south of the hive. In the first removal trial on 2–3 November, the training feeder was kept at its original location. In the subsequent three removal and misdirection trials, the training feeder was moved 1 m east to a position that experienced foragers had never visited (circle and arrows symbol indicates the switch). The final trial on 11 November was conducted with the training feeder back at the training site to determine if site bias occurring on 3–9 November could explain our results. No site bias was evident. The binomial probability and date of each trial are also given. In all trials, the feeders were scented with anise. Directional symbols as in Fig. 1

conducted in which newcomers chose between a pair of feeders based solely upon olfactory cues. During the free-foraging phase, ten experienced foragers fed at and recruited for the training feeder placed 100 m south of colony B and filled with 2.5 M anise-scented sucrose solution. During the removal phase, the assistant placed an identical control feeder (at which bees had never fed) 1 m east of the training feeder (Fig. 2). During the removal and misdirection phase, the assistant placed the control feeder at the original training site and placed the training feeder at the control site. One last removal experiment was conducted on 11 November to eliminate the possibility of site bias. The free-foraging phases also served as a control for site bias (Fig. 1). To avoid blocking incoming bees or biasing forager choice, the assistant sat behind and equidistant from both feeders (similar to Fig. 1).

H1 predicts that equal numbers of newcomers will choose both feeders if no bees are present on either feeder. Yet during the removal phases, significantly more newcomers always landed on the training feeder ( $P \leq 0.022$ , Fig. 2). H2 predicts that significantly more newcomers will arrive at the *site* of the training feeder. In the misdirection trials, the control feeder was placed at the *site* of the training feeder, yet significantly more newcomers always chose the training feeder over the control feeder ( $P \leq 0.022$ , Fig. 2). H3 predicts that significantly more newcomers will arrive at the training feeder regardless of its location. As H3 predicts, significantly more newcomers always chose the training feeder, even when this feeder was placed in a location at

which experienced foragers had never foraged ( $P \leq 0.022$ ). Thus newcomers were evidently guided by a scent beacon deposited on the training feeder by experienced foragers.

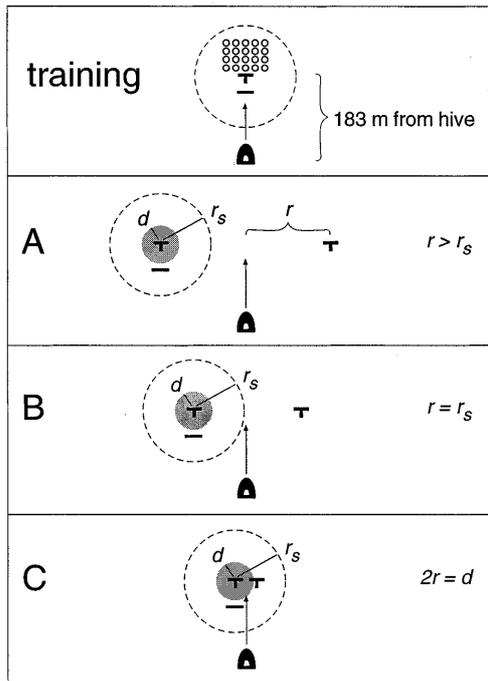
What is the effective radius of the scent beacon?

To determine if the scent beacon alone was a sufficient cue for newcomers to find the training feeder over longer distances, a training feeder was placed 100 m south of the hive and a control feeder 100 m north of colony B. Twenty foragers were trained to the south feeder and none to the north feeder. Five removal phase trials were conducted from 12 October to 30 November 1994, and 27 newcomers arrived at the training feeder and 27 at the control feeder ( $P = 1.00$ ). In all individual trials, significantly more newcomers failed to arrive at the training feeder ( $P \geq 0.29$ ). Thus equal numbers of newcomers arrived at both feeders, even though the training feeder had been visited and scent-marked by experienced foragers during the free-foraging phase that preceded each removal phase.

Thus the scent beacon had a limited effective radius. The following experiment determined this radius. Twenty marked bees were trained to a 2.5 M anise-scented sucrose feeder located 183 m northeast of colony B in 1996. At the end of a 30-min free-foraging phase, a removal phase was begun by capturing all bees leaving the hive. Once no foragers remained on the training feeder, an assistant moved this feeder a distance  $r$  to the left or right of the original training site. A second assistant placed an identical anise-scented control feeder at a distance  $r$  from the original training site but in the opposite direction from the training feeder (Fig. 3). During this movement process, both feeders were sealed in plastic containers to avoid scent leakage.

Once both feeders were in place and unsealed, the captured unmarked bees were released at the hive, and the assistants recorded the number of newcomers arriving on each feeder and the wind direction. Upon their arrival, all newcomers were immediately captured in plastic bags in order to prevent the choice of incoming newcomers from being biased by the presence of a bee on the feeder. The training and control feeder were initially 24 m apart. As usual, free-foraging and removal phases alternated, as were the positions of both feeders (left or right of the training site), to control for site bias, and assistants (changing who monitored the training feeder), to control for assistant-scent bias.

Assistants filled both feeders with identical quantities of anise-scented sucrose solution and each 60 min simultaneously added anise scent to the filter papers atop both feeders. Because both feeders were always equidistant from the hive and because newcomers did not possess directional information (eliminated by the removal procedure, Nieh 1997), I expected them to search in random directions for the feeder. I hypothesized that newcomers would follow two rules:



**Fig. 3** This figure illustrates the setup and rationale behind the scent radius experiments. *Open circles* represent experienced foragers trained to a location 183 m northeast of the hive (*solid hive symbol*). The *T-bars* represent feeders. The *arrows* show the flight path of *experienced foragers* from the hive to the training site. The distance between both feeders is  $2r$ , the effective radius of the scent beacon is  $r_s$ , and the distance at which the scent beacon is most effective is  $d$  (the radius of maximum discrimination). All feeders were scented with anise, although the effective radius of this scent is not shown, to avoid confusion. **A** The training stage. When  $r > r_s$ , newcomers should conduct a random search which will result in equal numbers of newcomers arriving at both feeders. **B** When  $r = r_s$ , more newcomers should begin to choose the training feeder over the control feeder. **C** When  $2r = d$  (the control feeder is just outside the radius of maximum discrimination) most newcomers should land on the training feeder. At some point within the *gray circle* ( $2r < d$ ), newcomers should fail to distinguish between the two feeders because the scent beacon effectively blankets both feeders (no scent contrast)

1. In the presence of food scent or scent beacon alone, the newcomer will fly to the zone of highest scent concentration.
2. In the presence of both scents, the scent beacon takes precedence and the newcomer will fly to the zone of highest scent beacon concentration.

When both feeders are quite far apart, newcomers beginning a random search from a position equidistant to both feeders should have an equal probability of encountering either the food scent or the scent beacon when the distance from the search initiation point to a feeder is much greater than the effective radius of the food scent or the scent beacon. By this condition and rule 1, equal numbers of recruits should arrive at both feeders. Thus the proportion of recruits landing on the training feeder ( $pt$ ) should equal 0.5. This prediction was empirically confirmed with the experiments previously described (in which the distance from the search initia-

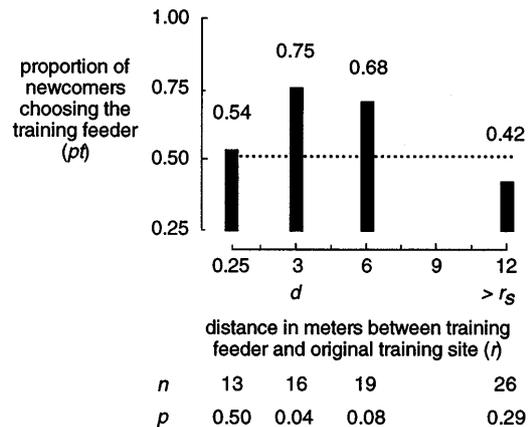
tion point, the hive, to each feeder was 100 m). In the experiment to measure the scent beacon's effective radius, the distance from the search initiation point (the hive) to the each feeder was 183 m (Fig. 3).

As the two feeders are brought closer together, the scent beacon will begin to overlap with the pure anise scent of the control feeder, and more newcomers should land on the training feeder (rule 2) because more newcomers will encounter both the scent beacon *and* the food scent ( $pt > 0.5$ ). Eventually, the scent beacon will equally blanket both feeders when both feeders are extremely close to each other, and equal numbers of newcomers should again land on the training feeder and the control feeder ( $pt = 0.5$ ).

Figure 3 illustrates the setup of the scent radius experiment. Figure 4 gives the observed results. The effective radius ( $r_s$ ) of the scent beacon equals the largest value of  $r$  for which  $pt = 0.5$ . Thus the effective radius was between 6 and 12 m. The maximum value of  $pt$  was 75% and therefore the radius of maximum discrimination ( $d$ ) was approximately 3 m.

How do they deposit the scent beacon?

Experienced foragers typically landed on the feeder and immediately began to forage. After foraging, a forager often used her metathoracic legs to groom her abdomen and wings and used her prothoracic legs to groom her head and mouth parts. While walking on the feeder, she sometimes dragged her abdomen on the surface and

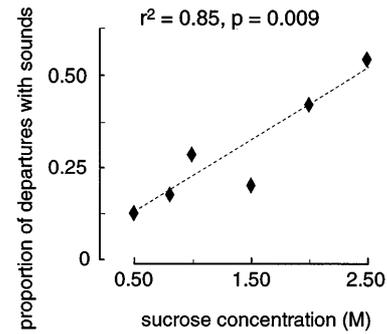


**Fig. 4** What is the effective radius of the scent beacon? This plot gives the proportion of newcomers choosing the training feeder ( $pt$ , represented by *solid bars*), the number of newcomers in each trial ( $n$ ), the 1-tailed binomial probabilities ( $P$ ), and the actual values of  $pt$  (shown above the corresponding bars). The *dashed line* indicates where  $pt = 0.5$  on the vertical scale. The maximum value of  $pt$  should occur at the radius of maximum discrimination ( $d$ ). As the distance between the two feeders is increased,  $pt$  should decrease until no further discrimination occurs. The critical distance  $r = r_s$  occurs when  $pt = 0.5$  as  $r$  is increased. This occurred at some distance between 6 m and 12 m, and thus the 12-m point is marked " $> r_s$ " to denote the limit of the effective scent radius. No winds were detected during any of these trials which were conducted from 7–12 August 1996

excreted a droplet of clear fluid from her anus. After foraging at high concentration sucrose solutions, her first action was often to spin clockwise or counter-clockwise on the feeder, and her last action was often to produce buzzing sounds.

Table 1 is a transition probability matrix of feeder departure behaviors summed over all sucrose concentrations (0.5–2.5 M). From this table, it is evident that the behaviors generally followed each other in this order: (1) spinning, (2) grooming, (3) abdomen dragging, (4) excreting anal droplets, and (5) producing sounds. When it occurred, sound production was always the last behavior performed by bees before they left the feeder.

The behavior of departing foragers varied with sucrose concentration. Table 2 shows that significantly fewer foragers dragged their abdomens ( $P = 0.042$ ) and excreted anal droplets ( $P < 0.0001$ ) as the concentration of sucrose increased. Significantly more foragers produced sounds and spun around as the concentration of sucrose increased ( $P < 0.0001$ ), and the proportion of departures with sounds increased linearly as sucrose concentration increased ( $P = 0.009$ , Fig. 5).



**Fig. 5** The relationship between the proportion of foragers who produced sounds upon their departure from the feeder and the concentration of anise-scented sucrose at the feeder is shown. The regression line (*dashed line*), correlation coefficient and regression  $P$ -value are shown

Is the scent beacon in the anal droplets?

In 1992, an experiment with colony A revealed that foragers excreted only a few anal droplets after collecting 2.75 M sucrose solution and many more anal droplets when the concentration of the sucrose solution was decreased to 1.0 M (Fig. 6). Foragers decreased their production of anal droplets once the feeder was refilled with 2.75 M solution. Thus increased anal droplet pro-

**Table 1** A transition probability matrix for the behaviors performed by departing foragers at the feeder over a range of sucrose concentrations (0.5 M–2.5 M) is shown. The highest probabilities in each row are given in *bold* and the number of behaviors observed ( $n$ ) is given at the end of each row. Sound production was the last behavior in all sequences, and this row consequently contains zero data. The matrix is obtained by taking a two-behavior reading frame and applying it sequentially to every behavioral state in every behavioral sequence. Thus the term “initial state” does not ne-

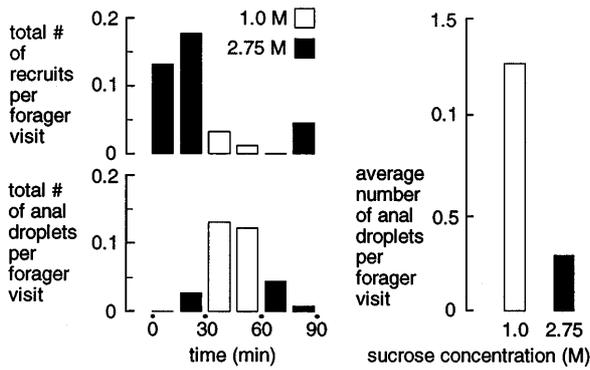
Initial state	Secondary state					$n$
	Spinning	Grooming	Abdominal dragging	Excreting anal droplets	Producing sounds	
Spinning	0.00	<b>0.67</b>	0.33	0.00	0.00	6
Grooming	0.05	0.00	<b>0.55</b>	0.11	0.29	76
Abdomen dragging	0.03	0.00	0.00	<b>0.77</b>	0.20	35
Excreting anal droplets	0.00	0.00	0.08	0.00	<b>0.92</b>	13
Producing sounds	–	–	–	–	–	0

**Table 2** How does the behavior of foragers at the feeder change as sucrose concentration changes? (A) The general trend (increased or decreased), the percentage of variance in behavior explained by the change in sucrose concentration (error sum of squares/total error), the value of the  $F$ -statistic from a one-way ANOVA, and the cor-

cessarily refer to the first behavior of the complete sequence. It is a relative term used to describe the first behavior in a pair of sequentially adjacent behaviors. The term “secondary state” refers to the behavioral state that foragers enter after the initial state. For example, some foragers performed the following sequence: (1) spinning, (2) grooming, and (3) abdomen dragging. In this example, when spinning was the initial state, grooming was the secondary state. When grooming was the initial state, abdomen dragging was the second state

responding  $P$ -value is given for each behavior. All behaviors were monitored at sucrose concentrations ranging from 0.5 M to 2.5 M. (B) The sucrose concentrations used and the number of visits monitored at each concentration are given *separately*

(A) Behavior	As sucrose conc. increased:	Variance explained by conc.	$F$	$P$	(B) Sucrose conc. used (M)	No. of feeder visits monitored per sucrose conc.
Spinning	Increased	8.6%	7.12	<b>&lt; 0.0001</b>	0.5	65
Grooming	Increased	2.2%	1.74	0.141	1.0	63
Abdomen dragging	Decreased	3.2%	2.51	<b>0.042</b>	1.5	66
Excreting anal droplets	Decreased	9.5%	7.97	<b>&lt; 0.0001</b>	2.0	43
Producing sounds	Increased	7.9%	6.48	<b>&lt; 0.0001</b>	2.5	71

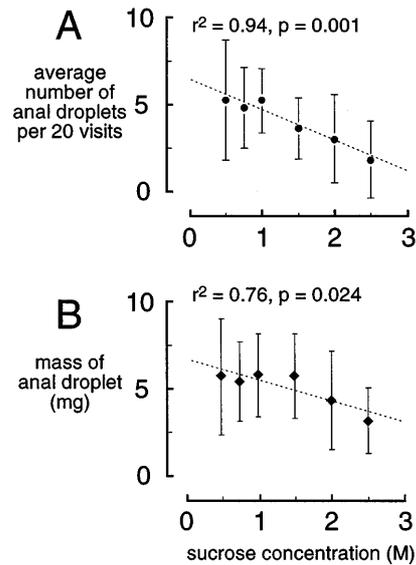


**Fig. 6** The relationships between recruitment and sucrose concentration and between anal droplet production and sucrose concentration are shown. *Open bars* represent 87 forager visits to 1.0 M anise-scented solution. *Solid bars* represent 105 forager visits to 2.75 M anise-scented solution

duction was not a function of time of day. After collecting a 1.0 M sucrose solution, foragers produced  $0.13 \pm 0.16$  anal droplets/visit, whereas they produced  $0.03 \pm 0.10$  droplets/visit after collecting a 2.75 M sucrose solution (Fig 6: 2-tailed test,  $M_{32,67} = 2176$ ,  $P < 0.0001$ ). Foragers therefore excreted significantly more anal droplets after collecting a more dilute sucrose solution.

During this same period, experienced foragers recruited significantly more newcomers when collecting the 2.75 M sucrose solution, the sucrose concentration that elicited the fewest anal droplets ( $\chi^2 = 35.8$ , 1 *df*,  $P < 0.0001$ ). Experienced foragers recruited 33 newcomers for a 2.75 M sucrose solution and only 4 newcomers for a 1.0 M sucrose solution (30-min presentations at each concentration, Fig. 6).

In 1994, experiments with colony B revealed that the average number of anal droplets per 20 visits decreased as the concentration of sucrose at the feeder increased (Fig. 7A). Sucrose concentration can explain 94% of the variance in the average number of anal droplets pro-



**Fig. 7** The relationships between **A** anal droplet size and sucrose concentration and **B** anal droplet weight and sucrose concentration are shown. Regression lines (*dashed lines*), correlation coefficients, and *P*-values are given. *Error bars* represent  $\pm 1$  SD

duced ( $P = 0.001$ ). The mass of each anal droplet also decreased as the sucrose concentration increased. Sucrose concentration can explain 76% of the variance in average anal droplet mass (Fig. 7B,  $P = 0.024$ ). Thus both the number and mass of anal droplets decreased as sucrose concentration increased.

Anal droplets did not attract foragers: 87 bees landed on the feeder baited with anal droplets and 93 bees landed on the feeder baited with blank vials (no significant differences,  $P_{\text{total}} = 0.354$ , Table 3). In three out of nine trials, significantly more foragers landed on the feeder baited with anal droplets ( $P \leq 0.041$ ). In two out of nine trials, significantly more foragers landed on the feeder baited with blanks ( $P \leq 0.012$ ). Thus anal droplets were evidently not the source of the scent beacon.

**Table 3** Are foragers attracted to anal droplets? Approximately equal numbers of foragers were attracted to the experimental feeder baited with anal droplets and to the control feeder baited with blanks. The droplets were either collected while a forager was feeding from a constant concentration of sucrose solution (2.5 M)

Date 1994	Sugar conc. at which droplet was collected (M)	Position of feeder baited with droplet	Number of bees attracted to anal droplet feeder	Number of bees attracted to blank feeder	<i>P</i>
13-Nov	2.5	East	12	8	0.503
15-Nov	2.5	West	4	16	<b>0.012</b>
16-Nov	2.5–0.5	West	7	13	0.263
14-Nov	2.5–1.0	West	17	3	<b>0.003</b>
17-Nov	2.75–1.0	West	15	5	<b>0.041</b>
19-Nov	2.75–1.0	West	6	14	0.115
19-Nov	2.75–1.0	East	3	17	<b>0.003</b>
20-Nov	2.75	West	8	12	0.503
24-Nov	2.75	East	15	5	<b>0.041</b>
		Total	87	93	0.354

or after the sucrose concentration was shifted (2.5–0.5 M). The latter droplets were collected while the forager was feeding at the lower concentration (0.5 M). All *P*-values are 2-tailed and were calculated from a binomial distribution (significant values given in *bold*). No detectable winds occurred during these trials

Is the scent beacon secreted into the sucrose solution?

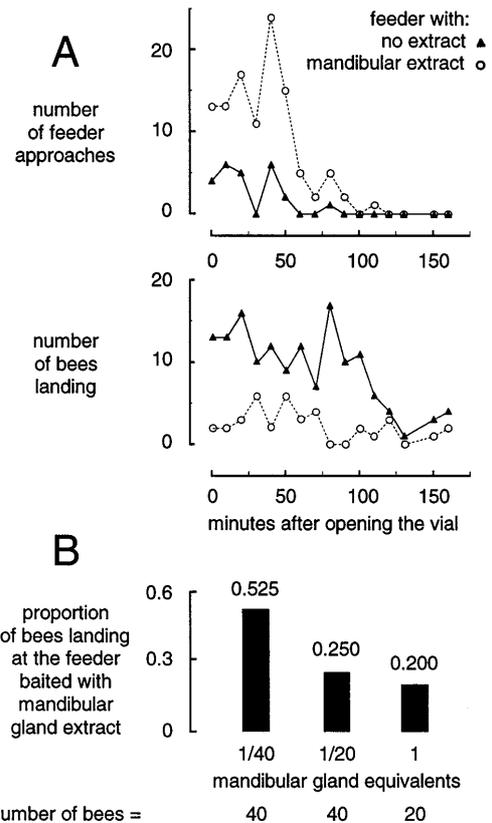
Table 4 shows that a total of 44 foragers landed at the feeder baited with vials of 2.5 M sucrose solution at which foragers had fed and a total of 38 foragers landed at the feeder baited with vials of fresh 2.5 M sucrose solution. Thus approximately equal numbers of foragers landed at both feeders (no significant overall difference,  $P_{\text{total}} = 0.78$ ). Only two trials exhibited significant choice biases. In one trial, significantly more foragers chose the baited feeder (baited feeder placed west,  $P < 0.0001$ ), but in the other trial, significantly more foragers chose the blank feeder (baited feeder placed east,  $P < 0.0001$ ). In all trials, there were no measurable winds at either feeder. Thus the sucrose solution was evidently not infused with the scent beacon.

Do mandibular glands produce the scent beacon?

In many stingless bees, including the *Melipona*, the mandibular glands secrete alarm pheromone (Roubik 1989). Appropriately, extracts from the mandibular glands of *M. panamica* foragers elicited alarm responses in other *M. panamica* foragers. Foragers approached the extract vials, hovering a few centimeters away while facing the open vials. This response was identical to the behavior of bees approaching a nestmate who released alarm pheromone at the feeder while being squeezed with tweezers.

Because the mandibular pheromone may become a scent beacon after its more volatile components have evaporated, I monitored the behavior of foragers over time. Alarm orientation behavior was strongest when the extract vials were first opened and decreased as the extract began to evaporate (Fig. 8A). In almost all cases, the forager oriented towards the feeder with the extract vials and then landed on the feeder with the blank vials. One approach is a bee hovering for at least 1s within 3 cm of a feeder. At all times, more foragers approached the feeder with extract vials than approached the feeder with blank vials (Fig. 8A; sign test:  $n = 47$ ,  $P < 0.0001$ ), and more foragers landed on the feeder with blank vials than landed on the feeder with extract vials (Fig. 8A; sign test:  $n = 47$ ,  $P < 0.0001$ ).

In separate trials, the concentration of mandibular gland extract was varied. During these trials, the pro-



**Fig. 8** Are foragers attracted to the mandibular gland extract? **A** Foragers oriented (*upper panel*) towards the feeder with vials of mandibular gland extract, but consistently landed (*lower panel*) on the feeder with blank vials at all times with non-zero data. I used the equivalent of 1 mandibular gland per vial (1/1 undiluted). *Open circles* represent the feeder with mandibular extract, and *solid triangles* represent the feeder with no mandibular extract (blank vials). **B** In separate attraction trials, I varied the concentration of mandibular gland extract presented. The proportion of bees landing on the extract-baited feeder approached 0.5 when the extract was most dilute and decreased when the extract was more concentrated. The corresponding numerical proportions are given above each bar. The number of bees involved is given below each bar. These trials were conducted on 17–25 November 1994. No winds were detected at the feeders during any of the trials

portion of bees landing on the extract-baited feeder approached 0.5 (no preference) when this feeder was baited with the *most dilute extract* and decreased with increasing extract concentration (Fig. 8B,  $\chi^2 = 20.9$ ,

**Table 4** Was the scent beacon contained in the sucrose solution at which foragers fed? Approximately equal numbers of foragers landed on the feeder with blanks and the feeder baited with vials containing sugar solution (at which 40 foragers had fed for 30 min).

Date 1994	Location of the baited feeder	No. at baited feeder	No. at blank feeder	$P$	Sig. more foragers at baited feeder?
14-Nov	West	10	10	1.00	No
16-Nov	West	1	19	<b>&lt; 0.0001</b>	No
14-Nov	East	13	7	0.26	No
16-Nov	East	20	2	<b>&lt; 0.0001</b>	Yes
	Total	44	38	0.78	No

The numbers of foragers at the baited and blank feeder are given as well as  $P$ -values (2-tailed) calculated from a binomial distribution (significant values given in bold). No detectable winds occurred during these trials

2 *df*,  $P < 0.0001$ ). Thus mandibular gland extract elicited no response at low concentrations and repelled foragers at higher concentrations. At higher concentrations, the alarm response consistently decreased over time, and at all times, more foragers preferred to land on the feeder *without* mandibular gland extract. Thus differential evaporation of the pheromone's components never led to attraction. Mandibular glands were therefore not the source of the scent beacon.

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## Discussion

The existence of a scent beacon

To summarize, three experiments reveal that *M. panamica* foragers deposit a scent beacon that influences the orientation of newcomers near the food source:

1. The removal and misdirection experiment shows that a scent beacon exists and influences newcomers within a distance of at least 1 m from the food source.

2. The long-distance removal experiment shows that the scent beacon does not guide newcomers to the training feeder when the control and training feeders are 200 m apart.

3. The effective-scent-radius experiment shows that the effective radius of the scent beacon is between 6 and 12 m. These last two experiments also demonstrate that the scent beacon cannot explain how newcomers find the training feeder at the correct three-dimensional location over long distances.

In addition, all three experiments provide information on how *M. panamica* foragers use the scent beacon.

1. In the removal and misdirection experiment, newcomers were prevented from orienting towards other foragers on the training feeder because all experienced foragers had been previously captured and any bee landing on either feeder was immediately captured (newcomers approaching while another bee was on within 5 m of the feeder were not counted). If newcomers did not orient towards a scent beacon, then they should have landed in equal numbers on both feeders or preferred to land on the control feeder during the misdirection trials (because this feeder was located directly at the training site). Yet significantly more newcomers always chose the training feeder, even when it was moved to a site at which experienced foragers had never foraged (Fig. 2). These results lead to two conclusions: (a) a scent beacon biased newcomer choice between the two otherwise identical feeders and (b) the removal procedure does not inherently disrupt orientation towards a scent beacon.

2. The removal experiment testing long-distance orientation to the scent beacon demonstrates that the scent beacon is effective only within a limited radius of the food source. Thus the scent beacon can only guide orientation near the food source. When the control and

training feeders were placed 100 m from the hive in opposite directions, equal numbers of newcomers arrived at both feeders during the removal experiments, even though the training feeder had been scent marked during the preceding free-foraging phases. Further details of this experiment are presented in Nieh (1997).

3. The experiment testing the effective radius of the scent beacon suggests that two simple rules can be used to model newcomer search and orientation strategies near the food source. In the effective-scent-radius experiment, the proportion of newcomers choosing the training feeder ( $pt$ ) was predicted to be 0.5 when both feeders were far apart and then increase as the distance between the control and training feeders decreased (rules 1 and 2, in Results section). A second prediction was that  $pt$  would peak as both feeders were moved closer together, and then decrease back to 0.5 as the distance between both feeders was further decreased. At  $r = 12$  m, roughly half of the newcomers (42%) chose the training feeder ( $P = 0.29$ ). At  $r = 6$  m, a majority of newcomers (68%) chose the training feeder ( $P = .08$ ). At  $r = 3$  m, significantly more newcomers (75%) chose the training feeder ( $P = 0.04$ ). (The earlier removal and misdirection experiment illustrated in Fig. 2 shows that 91% of newcomers found the training feeder when both feeders were separated by a distance of 1 m.) Finally at  $r = 0.25$  m, discrimination was lost and roughly half of the newcomers (54%) chose the training feeder ( $P = 0.50$ ). These results closely match the predictions of rules 1 and 2 and show that (a) the scent beacon's radius of maximal discrimination was between 0.25 m and 6 m and (b) the scent beacon had an effective scent radius between 6 and 12 m (for a scent beacon deposited by 20 foragers collecting a 2.5 M anise-scented sucrose solution for at least 30 min).

Because the scent beacon's concentration will be affected by feeder conditions (e.g., number of foragers, concentration of sucrose), feeder conditions will also influence the effective radius of the scent beacon. Nonetheless, the effective-radius experiment is informative because it demonstrates that the scent beacon has a limited effective radius, that this radius can be measured, and that simple scent-orientation rules can successfully predict the outcomes of newcomer searches near the food source.

What is the source of the scent beacon?

The scent beacon is evidently not deposited in anal droplets or secreted by the mandibular glands. Foragers preferentially recruited for higher sucrose concentrations (Nieh 1997), yet produced anal droplets that were heavier and more numerous for lower sucrose concentrations (Figs. 6, 7). These anal droplets also did not attract foragers: only 48% of foragers landed on the feeder baited with anal droplets ( $P = 0.354$ , Table 3). Thus anal droplets did not exhibit any of the charac-

teristics associated with a pheromone that attracts nestmates to a good food source.

My data suggest that these anal droplets are excess liquid (urine) excreted by the forager in order to lighten her load and to maintain her osmotic balance. Nicolson (1990:433) reported that “the liquid diet and high metabolic water production during flight in the carpenter bee *Xylocopa capitata*... causes a water excess” and results in the production of “copious dilute urine.” Thus as nectar becomes more dilute, urine excretions should be larger and more frequent. In fact, *M. panamica* foragers produced heavier anal droplets and produced them more frequently when they fed at more dilute sucrose solution.

Aguilar and Sommeijer (1996) proposed that anal droplets may attract foragers to a food source. They reported that *Melipona favosa* foragers produced anal droplets more frequently when the food source was farther away from the hive (from 9 to 49 m away in their experiments, 2.0 M honey solution), presumably because more distant feeders were more difficult for recruits to locate and thus required more scent marks. However, this relationship may also be explained by the cost of flying with excess weight. The heavier a bee is, the more energy she expends in flying back to the hive. By eliminating urine, bees can reduce their weight and thus decrease the flight cost. As the distance between feeder and hive increases, the cost of carrying excess weight may increase and result in more frequent urination.

In stingless bees such as *Scaptotrigona postica*, foragers rub their mandibles against a leaf or a blade of grass and thereby deposit a scent trail composed of mandibular gland pheromone (Lindauer and Kerr 1958, 1960). Kerr and Rocha (1988) observed *Melipona rufiventris*, *M. scutellaris*, *M. bicolor*, and *M. quadrifasciata* foragers rubbing their metathoracic legs together, their mesothoracic and prothoracic legs against their abdomen, and finally their mandibles against the borders of a leaf or stem after foraging. They argued that such mandibular rubbing deposits pheromone because it resembles the scent marking behavior of other stingless bees. Moreover, 92% of these rubbings occurred within 4 m of the feeder. Could *M. panamica* foragers secrete the scent beacon from their mandibular glands?

Curiously, mandibular gland pheromone is also the alarm pheromone for many stingless bee species (Roubik 1992). Pheromone context and concentration presumably play a role in allowing foragers of these species to exhibit an appropriate response. However, components of the alarm pheromone may evaporate differentially, leaving a residual mixture that foragers perceive as trail scent. Could such differential evaporation eventually produce a scent beacon from an alarm pheromone?

The mandibular gland extract experiment sought to test both these possibilities. However, *M. panamica* foragers only exhibited stereotypical alarm responses towards the mandibular gland extract. At the lowest concentration of extract (1/40 dilution), 53% of foragers landed on the extract-baited feeder. At the highest

concentration of extract (1/1 undiluted), only 20% of foragers landed on the baited feeder. Thus a higher concentration of extract caused foragers to *avoid* the baited feeder. Furthermore, more foragers consistently approached the baited feeder, yet a majority of foragers landed on the feeder with blank vials at all time intervals with non-zero data (Fig. 8). Thus differential evaporation did not convert the alarm pheromone into a scent beacon.

The source of the scent beacon consequently remains a mystery. It is possible that grooming behavior deposits the scent beacon, although not through mandibular gland excretions. *M. panamica* foragers may have groomed more frequently at the feeder as the sucrose concentration increased, although this increase was not significant ( $P = 0.141$ ). Behavioral analysis reveals that *M. panamica* foragers were more likely to spin after collecting higher concentrations of sucrose ( $P < 0.0001$ ). Perhaps foragers secrete a pheromone that they deposit while spinning on the food source.

Finally, it is possible that foragers do not directly secrete the scent beacon. While foraging, walking, dragging, spinning, and producing sounds on the feeder, hydrocarbons acquired through contact with the nest could be deposited on the feeder. Newcomers may therefore home in on a “hive odor” instead of a specific pheromone produced by foragers.

#### General implications of the scent beacon

The original experiments showing that *M. panamica* foragers can communicate distance, height, and direction (Nieh and Roubik 1995) revealed an extremely specific communication of distance and height. The scent beacon mechanism enables us to understand how this was achieved. In the array testing for *distance* communication, newcomers preferred the training feeder over the control feeder even when they were only 10 m apart (Fig. 3, Nieh and Roubik 1995). In the height experiments, newcomers preferred the training feeder over the control feeder when the training feeder was placed on the ground and the control feeder was placed 10 m *above* the training feeder (Fig. 4, Nieh and Roubik 1995). However, this discrimination disappeared when the training feeder was placed 40 m above the ground and the control feeder was placed 30 m above the ground in the same canopy tower (Fig. 5, Nieh and Roubik 1995). In these trials, roughly equal numbers of newcomers appeared at both feeders.

The scent beacon provides an explanation for the extremely specific site preferences of newcomers in the first two experiments and may explain why this preference was lost in the third experiment. At top of the canopy tower, 40 m, the rate of evaporation is much higher than on the forest floor because of higher temperatures (direct exposure to the tropical sun) and greater wind speeds (no obstructions to airflow from the dense canopy). Assistants reported that the artificial

scent added to the feeders evaporated more rapidly on the 40-m-high feeder than on the 0-m-high feeder. This higher rate of evaporation may have created a more diffuse scent beacon at the 40-m training feeder, thereby attracting newcomers to the 40-m training feeder *and* to the control feeder only 10 m below.

Thus at least two complementary systems exist to guide recruits: coarser-grained mechanisms that inform recruits of the general direction, distance, and height; and a finer-grained mechanism, the scent beacon, that guides recruits once they are near the food source. Other cues provided by the visual and acoustic stimuli of foragers on the food source may also attract nearby newcomers. In the free-foraging misdirection experiment, experienced foragers were generally present on the feeders when newcomers made their choices and 100% of newcomers landed on the training feeder (Fig. 1). In the removal and misdirection experiment, no other bees were present on the feeders when newcomers made their choices and only 91% of newcomers landed on the training feeder (Fig. 2).

It seems reasonable to expect that a recruitment system will employ multiple sources of information to optimize recruitment success. Multiple sources can enhance accuracy and provide backup in case one information source is weak or lost. In the past, some discussions of honey bee communication have been polarized by an emphasis upon odor orientation or dance communication (see Gould 1976 for review), although the importance of both components was originally recognized by von Frisch (1967). I hope to avoid confusion by clearly stating that *multiple sources* of information, delivered inside and outside the hive, inform the recruitment of *M. panamica* foragers (Nieh 1997). Recruits *cannot* orient to a scent beacon over long distances but *can* orient to a scent beacon when they are 6–12 m from the food source. Scent has a role, but is not the entire tale.

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