

The communication of food location by a primitive stingless bee, *Trigona carbonaria*

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Summary

The stingless bees (Hymenoptera: Apidae: Meliponinae) reportedly possess communication systems with a broad range of complexity. However, prior research has focused on species that can accurately communicate food location. Little is known about species with a weak ability to communicate food location. We therefore examined the spatial communication abilities of a putatively primitive stingless bee, *Trigona carbonaria*. We trained foragers to one feeder (the experimental feeder) and set out an array of identical control feeders to test the communication of direction and distance. Recruits could find the food source at the correct *direction*, but this was influenced by orientation to food odor and a favorable wind direction. In trials with scented feeders, significantly more newcomers (71%) arrived in the correct direction when the experimental feeder was directly *upwind* from the nest. When the experimental feeder was *downwind* from the nest, a non-significant majority of newcomers (51%) arrived at the experimental feeder. However, orientation to food odor is not essential, since significantly more newcomers arrived at the experimental feeder in the unscented direction trial with rapid recruitment (50 newcomers/hours, 195 forager visits per hour). Experienced foragers did not appear to communicate *distance* because newcomers (61%) generally preferred the closest feeder to the nest, even in the unscented distance experiments. Overall, our results suggest that recruits can orient to the scent of the food source and may also orient to a forager-deposited pheromone at the food source or follow experienced foragers for part of the distance to the food source.

Introduction

The stingless bees are taxonomically diverse (Michener 1990) and reportedly possess a wide range of recruitment communication strategies with a broad spectrum of complexity (Lindauer & Kerr 1958; Kerr 1960, 1969; Kerr et al. 1963; Roubik 1989). This diversity provides an excellent opportunity to study alternative foraging strategies and the evolution of communication in highly social bees. Yet the ability of foragers to recruit has only been well documented in a few species, and generally for those species, such as *Scaptotrigona postica* and *Melipona panamica*, that can communicate food location and exhibit more complex recruitment behaviors (Lindauer & Kerr 1960; Esch et al. 1965; Esch 1967; Kerr et al. 1981; Kerr 1994; Nieh & Roubik 1995, 1998; Nieh 1998a, b). We should therefore begin to carefully assess the capabilities of species with presumably primitive communication systems before addressing the adaptive value of alternative foraging strategies and the evolution of recruitment communication.

We consequently focused our attention on the recruitment abilities of a primitive stingless bee, *Trigona carbonaria*, in which the communication of distance and direction had not been studied. Yamane et al. (1995) suggest that this bee is relatively primitive since it retains ancestral traits characteristic of the subgenus *Tetragonula*: synchronous cell construction, an exclusively batched oviposition process, synchronous food provisioning in brood cells, generalized agitation at food provisioning, and cell operculation clearly differentiated into distinct phases. Moreover, many of these traits are also found in the Neotropical genus *Nannotrigona* (Yamane et al.

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1995) in which foragers are thought to have a primitive communication system that does not indicate food location (Kerr 1969).

T. carbonaria is one of 12 Australian stingless bee species found in New Guinea and in Australia from north-western Queensland to southern New South Wales (Cardale 1993; Dollin et al. 1997). Colonies of 2,500–3,000 workers (each approximately 4.4 mm in length) normally live in hollows formed inside standing trees with an average diameter of 55 cm (Cardale 1993). Bartareau (1996) reported that *T. carbonaria* foragers can rapidly recruit to artificial feeding stations, and we therefore conducted feeder array experiments to determine if these foragers can communicate the direction or distance to a good food source.

We conducted these experiments with the purpose of establishing whether or not *Trigona carbonaria* foragers can recruit nestmates to a specific location. Our data has also enabled us to eliminate some potential communication mechanisms and has suggested other communication mechanisms to be examined in future research. We therefore wish to clarify our understanding of the term “communication”. Throughout this paper, we adopt Wilson’s (1975: 10) definition of communication: “action on the part of one organism (or cell) that alters the probability pattern of behavior in another organism (or cell) in an adaptive fashion.” By this definition, we include communication mechanisms that deposit pheromones at the food source, mechanisms that bring back and advertise the scent of the food source, and non-odor based mechanisms involving sounds or motions inside the nest.

Methods

Study site and bee colonies

We used two colonies of *T. carbonaria*. Colony A was housed in its original log nest and Colony B was housed inside a wooden box nest (21 cm × 21 cm × 28 cm, design in Heard 1998). Colony A came from a site 10 km SW of the town of Atherton, colony B from a site 6 km SSE of Herberton. We were unable to measure the population size of these colonies, but *T. carbonaria* colonies generally have 2,500–3,000 bees of which approximately 1,200–1,600 are adult foragers (Bartareau pers. comm.).

We first used colony A and then, upon its removal, colony B. The study site was a grass paddock bounded by trees in the north and south and a small dam in the west (Fig. 1). This site was located in Atherton in north-east Queensland (145° 27.5'E, 17° 14.9'S) approximately 720 m above sea level. We conducted these experiments in January 1998.

Training and marking bees

To train bees, we injected a small quantity of sucrose solution into the nest and presented a 6.7 cm diameter grooved-plate sucrose feeder at the entrance (feeder de-



Fig. 1. Aerial view of the research site and positions of the nest and feeders 150 m from the nest. The letter “N” marks the nest site and asterisks mark the feeder sites. On the west side, the research site is bordered by a small body of water divided by a dam. The upper asterisk indicates a position directly north of the nest. In any given direction trial, we used only 3 of these feeder sites. In the sealed-colony control experiment, we used all 4 of these feeder sites. (Photograph source: Queensland Department of Natural Resources Land Services).

sign in von Frisch 1967). After a few foragers discovered the feeder, we moved it 1 cm away, leaving a gap over which the foragers were forced to fly. We gradually moved this feeder (the experimental feeder) to the desired location. During training, we used either acrylic paints or shellac mixed with powdered paint pigments to mark the thorax or each bee visiting the feeder. We marked each forager with one of six different colors while she fed at the feeder. We could not uniquely mark all foragers because the thorax (<1.5 mm in diameter) was too small to allow multiple color marks, even with extremely fine brushes (size 0000).

Feeder arrays

The feeder stands consisted of 1.4 m high steel rods inserted into the ground (design in Bartareau 1996). We tied a 30 cm long piece of yellow flagging tape to each stand. Four metal prongs at the top of each rod held a 12 cm × 16 cm rectangle of white styrofoam upon which we placed a circle of yellow paper and then the transparent glass and plastic feeder. All feeders contained identical sucrose concentrations (0.5, 1.0, or 2.5 M). Because the recruitment rate varied substantially in some trials (probably because of variation in natural food source availability), we varied the sucrose concentrations in order to maintain a constant rate of recruitment and to avoid exhausting the colony of all foragers during time periods with an extremely high recruitment rate (method discussed in von Frisch 1967). All sucrose solutions were *unscented*. For scented feeders, we placed a 19.6 cm²

circle of Whatman filter paper under the circle of yellow paper and added 20 μ l of lavender oil with a calibrated micro-pipette. We renewed scents once each 30 min. We used two-way radios to coordinate the simultaneous switching of sucrose concentrations and the addition of scent in the scented experiments. When switching from scented to unscented experiments, we used new feeders and yellow paper disks and washed and dried the equipment at each of the feeder sites.

All feeders were identical, except that foragers could only feed at and recruit for the experimental feeder. We immediately marked all foragers visiting the experimental feeder or captured them with aspirators. Each aspirator consisted of two flexible vinyl tubes (1 cm inner diameter, each tube approximately 25 cm long) inserted into a clear plastic cylinder (7 cm \times 8 cm). We covered the distal end of the mouthpiece tube with fine mesh and lined the cylinder walls with tissue paper to cushion aspirated bees.

At the control feeders, feeder monitors used aspirators to capture all bees as soon as they landed. Thus no bees could recruit for the control feeders, and all unmarked bees (newcomers) had no prior experience with any feeder. Newcomers became experienced foragers once they landed on a feeder (our definition).

Each 10 min, we counted the number of experienced foragers that landed on the feeder during a 2 min interval. We allowed only five to eight experienced foragers to feed at the experimental feeder each 2 min (2.5–4.0 visits min^{-1}). When the visitation rate exceeded 4.0 visits

min^{-1} , we removed excess foragers with an aspirator. When the visitation rate fell below 2.5 visits min^{-1} , we painted newcomers instead of aspirating them.

At the completion of experiments at each training site, we used aspirators to capture all marked foragers coming to the experimental feeder, waited 20 min after capturing the last forager (to insure that we had captured all foragers for the old feeding site), placed a feeder close to the nest, and began the training procedure again with a new set of foragers. Bees survived in the aspirators for several days and were only released at the end of all experiments with each colony. We trained a new set of bees for each experiment, and all foragers recruited in previous experiment were retained in the aspirators to prevent the communication of control feeder sites. We used one colony at a time and we waited after dusk (when all foragers had returned) before sealing and replacing colony A with colony B.

We employed two techniques to determine if all foragers came from the colony under study. First, we counted fights at the feeders since workers from different colonies will fight when they meet at the same food source. Second, we sealed off our study colony and then set out the feeders as normal to see if bees from other colonies would arrive. On the evening of Jan 27, we sealed colony B (this insured that all bees were inside the nest), and on Jan 28 (from 0802 to 0847 hours) we monitored four scented feeders filled with 2.5 M sucrose solution at sites 150 m north, south, east, and west of the nest (Fig. 1).

Table 1. Results of experiments testing the communication of direction. The wind direction is given in degrees (0° = North, 90° = East, 180° = South, 270° = West) and words. The locations of the experimental and control feeders are given above the trials comprising each experiment. The results of the G-test and P-values are also given (significant values in bold, $\alpha = 0.05$).

Scented feeders?	Sucrose conc.	Date	Trial times	Average wind direction	Number of recruits*				
					E (exp)	S (ctrl)	W (ctrl)	G adj	P
Experiment 1									
yes	1.0 M	22-Jan	1415–1445	113° E	18	4	2	17.61	0.0001
yes	1.0 M	23-Jan	0949–1019	94° E	11	8	1	9.81	0.0074
yes	2.5 M	23-Jan	1019–1049	94° E	12	2	2	11.15	0.0038
yes	1.0 M	23-Jan	1049–1119	94° E	13	3	0	18.92	0.0001
Experiment 2					W (exp)	S (ctrl)	E (ctrl)		
yes	1.0–2.5 M	24-Jan	0930–1100	95° E	12	3	2	9.65	0.0080
yes	2.5 M	24-Jan	1100–1130	82° E	7	0	10 (1)	14.94	0.0006
yes	2.5 M	24-Jan	1130–1200	90° E	10	1	7	8.48	0.0144
yes	2.5 M	24-Jan	1200–1230	90° E	6	3	8	2.30	0.3171
Experiment 3					S (exp)	W (ctrl)	N (ctrl)		
no	2.5 M	25-Jan	1712–1742	120° ESE	14	0	3	20.70	<0.0001
no	2.5 M	25-Jan	1742–1812	80° E	30	1	2	47.62	<0.0001
Experiment 4					N (exp)	W (ctrl)	S (ctrl)		
no	1.0 M	20-Jan	1418–1448	220° SW	2	2	1	0.39	0.8247
no	2.5 M	26-Jan	1448–1518	240° SW	5	2 (1)	1	2.71	0.2579
no	2.5 M	26-Jan	1518–1548	230° SW	2	1	1	9.40	0.8172
no	2.5 M	26-Jan	1548–1618	230° SW	2	1	0	2.27	0.3217

* number of experienced foragers landing at the control feeders given in parentheses

Table 2. Results of experiments testing the communication of distance. The wind direction is given in degrees (0° = North, 90° = East, 180° = South, 270° = West) and words. In each trial, all feeders were placed in the same direction. The trials are organized into three experiments that correspond to the placement of the experimental feeder in three different cardinal directions. The G-test was conducted with the null hypothesis that equal numbers of recruits would arrive at all feeders. The critical alpha levels are given above each column of test results. Significant values are shown in bold.

Scented feeders?	Sucrose conc.	Date	Trial times	Average wind direction	Direction of the feeders	Number of recruits*				$\alpha = 0.05$		$\alpha = 0.0056$		
						50 m (ctrl)	150 m (exp)	200 m (ctrl)	Equal numbers at all 3 feeders?	G adj	P	Equal numbers at 50 m and 150 m?	G adj	P
Experiment 1														
yes	1.0 M	22-Jan	1500–1530	113° ESE	E	4	4	0	5.99	0.0500	0.00	1.0000		
yes	2.5 M	23-Jan	1130–1200	94° E	E	24 (3)	21	6	15.00	0.0006	0.74	0.3883		
yes	1.0 M	23-Jan	1200–1230	80° E	E	47 (1)	52	1 (2)	60.33	<0.0001	0.16	0.6899		
Experiment 2														
yes	2.5 M	24-Jan	1238–1308	84° E	W	20 (3)	13	0	31.43	<0.0001	2.78	0.0957		
yes	2.5 M	24-Jan	1308–1338	84° E	W	24	11	1	25.91	<0.0001	4.88	0.0272		
Experiment 3														
no	1.0 M	26-Jan	0838–0908	66° ENE	S	8	4	0	10.51	0.0052	1.30	0.2533		
no	2.5 M	26-Jan	0908–0942	290° W	S	16	9	0	21.68	<0.0001	1.95	0.1629		
no	2.5 M	26-Jan	0942–0958	320° NNW	S	33	5	3	38.40	<0.0001	22.79	<0.0001		
no	0.5 M	26-Jan	0958–1028	193° S	S	35	6	0	55.0	<0.0001	22.43	<0.0001		

* number of experienced foragers landing at the control feeders given in parentheses

Direction and distance experiments

For the *direction* experiments, we set up three identical feeders 150 m from the nest. We trained foragers to only one feeder (the experimental feeder). We always placed one control feeder directly opposite from the experimental feeder. Thus if we placed the experimental feeder north of the nest, we placed one of the control feeders south of the nest. For the *distance* experiments, we placed all feeders in the same direction from the nest. The experimental feeder was 150 m from the nest and the control feeders were 50 m and 200 m away from the nest. We generally conducted trials for 30 min, although one distance trial lasted for 15 min because of an extremely high recruitment rate, and one direction trial lasted for 90 min because of an extremely low recruitment rate (data given in Tables 1 and 2).

In all trials, an observer continuously monitored the wind direction with a compass and a 30 cm strip of plastic flagging tape attached to a feeder stand. The observer noted all changes in wind direction. We subsequently calculated the average wind directions in each trial with the wind directions weighted by time. Thus if an east wind blew for 20 min and then shifted to the west for the last 10 min of a trial, we weighted the east wind by a factor of 2 relative to the west wind. From Jan 22–25, the wind blew steadily with minor variations from the east. On Jan 26, the wind shifted from the east to the south at 0958 hours and then blew from the southwest from 1418–1618 hours. Throughout this paper, we give the *downwind* wind direction.

Statistics

For the distance and direction experiments, we use G-tests to analyze the distribution of newcomers arriving at the feeders (Sokal and Rohlf 1995). In reporting the results of individual replicated G-tests, we give the G_{ADJ} value (Williams correction to reduce type I error). For reporting the overall results of replicated tests, we give G_P (all data pooled) and G_H (interaction test). Where appropriate, we apply a Bonferroni correction to carry out tests at a critical α -level, where $\alpha = 0.05/k$ and k equals the number of tests (Sokal and Rohlf 1995). In such cases, we report the α -level with the P -value, and only consider the test significant if $P \leq \alpha$. We report all P -values less than 0.0001 as $P \leq 0.0001$ and averages as mean ± 1 SD.

Results

Identity of foragers

Two lines of evidence suggest that all of the foragers coming to our feeders were from the subject colony. (1) We observed no fighting between foragers at the feeders in any of our 14 direction or 9 distance trials. (2) In our sealed-colony control experiment, no foragers came to any of the four scented feeders

placed at the 150 m feeder locations. During this experiment (from 0802 to 0847 hours), the temperature increased from 23.4° to 26.1 °C and light levels were quite high since the sun had risen at 0615, *T. carbonaria* foragers begin to forage at temperatures above 18 °C (Wagner and Dollin 1982) and at light levels greater than 15 W m⁻² ("perceived by the human eye as the first light of day observed at dawn," Heard & Hendrikz 1993: 351). Heard & Hendrikz (1993) also reported that *T. carbonaria* flight activity peaked during January between 0800 and 0830 hours. Thus no bees from other *T. carbonaria* colonies discovered our feeder during the sealed-nest control experiment, even though we conducted this experiment under peak January foraging conditions.

Recruitment rate

For each recruitment trial, we calculated the recruitment rate by counting all newcomers arriving at the experimental and control feeders and dividing by the trial duration. The overall recruitment rate was 0.877 ± 2.33 recruits · min⁻¹ (maximum = 3.33 recruits · min⁻¹, minimum = 0.10 recruits · min⁻¹, *N* = 22 trials). Thus, on average, an experienced forager visited the experimental feeder 3.7 times before a newcomer arrived at any feeder.

Feeder discovery rate in the absence of recruitment

In four 20 minute control trials conducted on January 23, 24, 25, and 26, we removed all the marked foragers and waited with all four feeders set out in the array testing directional communication. During these trials, no recruits arrived at any feeder. Thus the rate at which newcomers discovered our feeders in the absence of experienced foragers recruiting for a feeder was zero.

Scented direction experiments

We organized the results of the scented direction experiments into four groups of trials (Table 1). Each group corresponds to the placement of the experimental feeder in a different cardinal direction. No significant heterogeneity exists within each group (all $P \geq 0.267$) and thus we have pooled the data from individual trials into four groups in Fig. 2 and Fig. 3. Henceforth, we will refer to each group of trials as a separate direction experiment.

Figure 2 shows the results of our direction experiments with scented feeders. In Fig. 2A, the experimental feeder is *upwind* from the nest and in Fig. 2B, the experimental feeder is *downwind* from the nest. In both cases, more recruits arrived at the experimental feeder and the distributions of newcom-

ers arriving at all 3 feeders are significantly non-uniform (all $P < 0.0001$).

However, wind direction influenced the spatial distribution of newcomer arrivals (Fig. 2B). There is significant heterogeneity between the pooled-upwind and pooled-downwind trials ($G_{H2} = 25.81$, $P < 0.0001$). The trend is clearest in comparisons of newcomers at the experimental (EXP) feeder and the feeder in the opposite direction (OPP). Significantly more recruits arrived at the EXP feeder when the feeder was *upwind* of the nest ($G_{ADJ 1} = 47.1$, $P < 0.0001$, $\alpha'' = 0.025$). There was no significant difference in the number of newcomers arriving at the EXP and OPP feeders when the EXP feeder was *downwind* from the nest ($G_{ADJ 1} = 0.77$, $P = 0.379$, $\alpha'' = 0.025$), although more newcomers still arrived at the EXP feeder. Thus wind direction altered newcomer arrival patterns in the scented direction experiments.

Unscented direction experiments

Figure 3 shows the results of our direction experiments with unscented feeders. In both cases, the wind direction was approximately perpendicular to the feeder-nest axis. The distribution of newcomers arriving at all three feeders was significantly non-uniform when the EXP feeder was *south* of the nest ($G_{ADJ 2} = 66.9$, $P < 0.0001$, $\alpha'' = 0.025$, Fig. 3A). However it was not significantly different from a uniform distribution when the EXP feeder was *north* of the nest ($G_{ADJ 2} = 4.71$, $P = 0.091$, $\alpha'' = 0.025$, Fig. 3B). A five-fold difference in recruitment exists between both of these trials (50 newcomers/hour when the EXP feeder was north vs. 10 newcomers/hours when the EXP feeder was south, Table 1).

In the unscented direction experiments, comparisons of newcomers at the EXP feeder and the OPP feeder reveal that significantly more newcomers arrived at the EXP feeder under conditions favoring rapid recruitment (50 newcomers/hour, $G_{ADJ 1} = 35.3$, $P < 0.0001$, $\alpha'' = 0.025$, Fig. 3A) than under slow recruitment conditions. However, a non-significant majority of newcomers arrived at the EXP feeder under slow recruitment conditions (10 newcomers/hr, $G_{ADJ 1} = 4.69$, $P = 0.030$, $\alpha'' = 0.025$, Fig. 3B). Thus although newcomers can search in the correct direction for an unscented feeder, they evidently do not do so at low levels of recruitment (10 newcomers/hour).

Distance experiments

In the distance experiments, newcomers generally preferred the closer feeder (Table 2). Overall, 61% of newcomers landed at the 50 m control feeder, 36% landed at the 150 m experimental feeder,

Scented Feeders

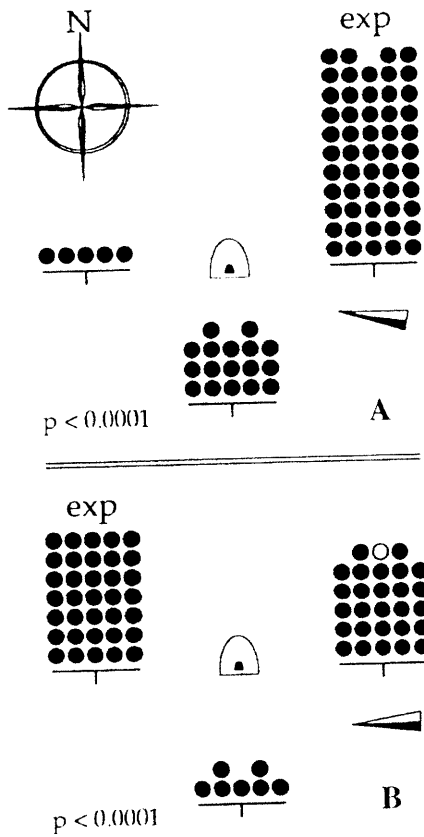


Fig. 2. Results of the direction experiment with scented feeders. The pooled results from all trials with the experimental feeder in the East (A) and then in the West (B) are shown. All feeders are 150 m from the nest depicted in the center. Filled circles represent newcomers. The open circle indicates a marked forager that was captured at a control feeder. The arrowheads indicate the average wind direction. The P -values indicate if the distributions are significantly non-uniform.

and 3% landed at the 200 m control feeder. To analyze these results, we first examined the data from all three feeders and then focused on the two closest feeders, where 97% of recruits arrived. In all nine trials, the distribution of newcomers arriving at all three feeders was significantly non-uniform (all $P \leq 0.050$). In seven out of nine trials, more newcomers arrived at the 50 m control feeder. In one trial, equal numbers of newcomers arrived at both feeders. In the remaining trial, more newcomers arrived at the 150 m control feeder, although this distribution was not significantly different from a uniform distribution ($P = 0.69$).

The presence of scent appeared to change the proportion of newcomers arriving at the closest feeder. In the scented trials, $55.4 \pm 8.2\%$ of newcomers arrived at the 50 m control feeder. In the un-

Unscented Feeders

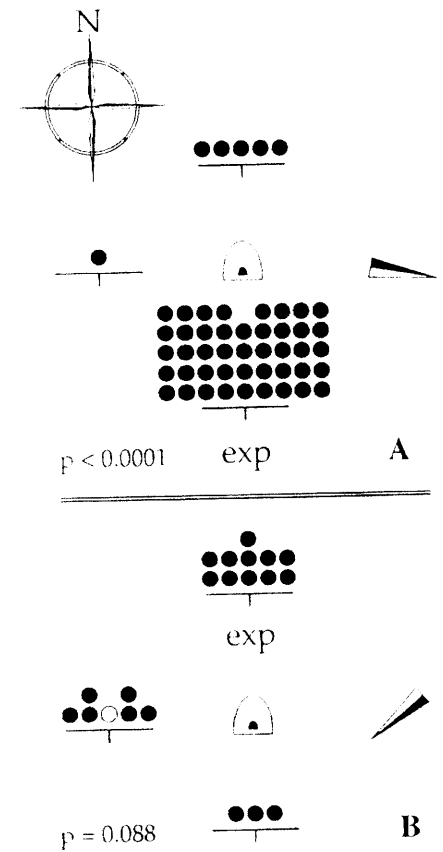


Fig. 3. Results of the direction experiment with unscented feeders. The pooled results from all trials with the experimental feeder in the South (A) and then in the North (B) are shown. All feeders are 150 m from the nest (depicted in the center). Filled circles represent newcomers. The open circle indicates a marked forager that was captured at a control feeder. The arrowheads indicate the average wind direction. The P -values indicate if the distributions are significantly non-uniform.

scented trials, $74.1 \pm 9.0\%$ of newcomers arrived at the 50 m control feeder. We found significant heterogeneity within the scented trials and the unscented trials ($G_{H2} = 29.1$, $P < 0.0001$) due to the small but variable number of newcomers arriving at the 200 m feeder. We therefore proceeded to analyze data from the 50 m and the 150 m feeders, where 97% of newcomers arrived.

When one considers only the data from the 50 m and 150 m feeders, the scented-trials data is homogenous ($G_{H4} = 5.91$, $P = 0.206$) and the unscented-trials data is homogenous ($G_{H3} = 6.60$, $P = 0.081$). However the two data sets are heterogeneous ($G_{H1} = 19.9$, $P < 0.0001$), and thus there is a significant interaction between food scent and the distribution of newcomers at the two closest feeders (assuming that the newcomer search strategies of

colony A and colony B were the same). With scented feeders, no significant difference exists between the number of newcomers arriving at both feeders (119 bees at 50 m, 101 bees at 150 m; $G_{P,1} = 1.47$, $P = 0.2247$, $\alpha'' = 0.0083$). With unscented feeders, significantly more newcomers arrived at the feeder closest to the nest (92 bees at 50 m, 24 bees at 150 m, $G_{P,1} = 24.8$, $P < 0.0001$, $\alpha'' = 0.0083$).

Discussion

General results

Our experiments reveal that experienced *Trigona carbonaria* foragers can direct a majority of newcomers to a food source at a specific direction from the nest. Since no newcomers arrived at any of the feeders in the absence of experienced foragers, the observed newcomer arrival patterns were due to recruitment. In 12 out of 14 direction trials, the greatest proportion of newcomers were recruited to the experimental feeder. However, the communication of direction was highly influenced by the scent of the food source, particularly when the wind blew directly from the food source to the nest (Fig. 2). Nonetheless, the unscented direction experiments show that the scent of the food source is not necessary for correct newcomer orientation. In both unscented direction experiments, more newcomers arrived at the experimental feeder than arrived at the two identical control feeders (Table 1). This difference was significant in the trial with a high recruitment rate (50 newcomers/hour), but not in the trial with a low recruitment rate (10 newcomers/hour). Under low recruitment conditions, only 3.7 times more newcomers arrived at the experimental feeder than at the control feeder. One possible explanation is that foragers adopt an alternative foraging or communication strategy to spread out recruits under conditions resulting in low recruitment (such as an abundance of natural food sources). This would allow recruits to discover the food at new locations. Honeybees may also adaptively use communication "inaccuracy" (divergence in the waggle run angle) to allow recruits to discover new food sources at nearby locations (Towne & Gould 1988, Weidenmüller 1998).

T. carbonaria recruits evidently did not search for the food source at the correct distance. In all three distance experiments, significantly more newcomers failed to arrive at the experimental feeder. These experiments do not exclude the possibility that experienced foragers communicate distance to recruits, but they suggest that recruits do not have or do not use such information to inform their search patterns when faced with multiple identical food sources in the environment. With scented

feeders, we observed newcomers approaching downwind from the feeder, often flying in a zigzag oriented towards the feeder. When the feeders were unscented, newcomers flew near the ground, circled around the feeder, and appeared to take more time to finally land and find the feeding dish on the styrofoam block. The slower search patterns of newcomers orienting to unscented feeders could also account for the differences between the scented and unscented distance experiments. In the scented distance experiment, approximately equal numbers of newcomers arrived at the 50 m and at the 150 m feeder (119:101 bees). However, a majority of newcomers arrived at the 50 m feeder (92:24 bees) when we used unscented feeders. Thus a potentially more dispersed search pattern caused by using unscented feeders may have resulted in more newcomers encountering the closer feeder.

At this point, we would like to consider the effect of using different colonies in our experiments. We conducted the scented experiments with colony A and the unscented experiments with colony B. Thus comparisons between scented and unscented experiments are based upon the assumption that basic mechanisms of communication are conserved within a species, and we have explicitly stated this assumption in the one case where we made such a comparison (see results of the distance experiments). This assumption has proven valid in several other stingless bee species. Nieh & Roubik (1995, 1998) conducted similar feeder array experiments with 3 different colonies of the stingless bee *Melipona panamica* and found no differences in their ability to communicate the distance, direction, or height of a food source. Johnson & Hubbell (1974) and Nubbell & Johnson (1978) also used artificial feeders to examine the foraging strategies of six different *Trigona* species. They found consistent differences between the foraging strategies of different species, but no differences between colonies of the same species.

Potential communication mechanisms

The purpose of this paper is to establish the spatial communication abilities of *Trigona carbonaria*, but our results also shed light on potential communication mechanisms by limiting the number of possible mechanisms. First, *T. carbonaria* foragers evidently do not lead recruits directly to the food source since this mechanism should not be sensitive to wind direction and should lead a majority of recruits to the feeder at the correct direction and distance. Second, *T. carbonaria* foragers do not appear to leave a scent trail. Stingless bees that deposit scent trails do so on their return flight back to the nest by landing every few meters and rubbing a

pheromone onto grass or leaves (Lindauer and Kerr 1958; Kerr 1960; Kerr et al. 1981). *T. carbonaria* foragers flew directly from the feeder towards the nest at a visually estimated height of 4–5 m during 57 observed departures. Even during recruitment peaks, we did not observe foragers landing to lay a scent trail. Moreover, such a scent trail would remain to indicate the correct direction even given an adverse wind direction or an unscented food source. Our data show that directional communication is strongly affected by wind direction and the use of unscented food sources. Thus the following possibilities remain: (1) recruits orient to the scent of the food source; (2) recruits orient to a pheromone deposited by experienced foragers near the food source; and (3) recruits follow experienced foragers for part of the distance to the food source (partial piloting).

(1) Newcomers appear to orient towards food scent because significantly more newcomers arrived at the experimental feeder when it was *upwind* from the nest, but not when it was *downwind* from the nest (Fig. 2). When the experimental feeder was downwind from the nest, a non-significant majority of newcomers arrived at the experimental feeder (35 newcomers at the downwind experimental feeder and 27 newcomers at the upwind control feeder, Fig. 2B). Newcomers also had much more difficulty finding unscented feeders than finding scented feeders. They took more time to land and flew around more slowly in wider arcs around unscented feeders. Recruits presumably learn the scent of the food source inside the nest by contacting foragers who have scent adhering to their bodies or by receiving scented food samples.

(2) Since a scented food source is not necessary in order for newcomers to arrive at the correct *direction* (under conditions favoring rapid recruitment), foragers may also deposit pheromone marks on the food. Our *distance* experiments also suggest that recruits do not orient towards such a pheromone when they are far away from the food source. Long-distance pheromone orientation should have resulted in more newcomers arriving at the 150 m experimental feeder. Instead, only 36% of newcomers arrived at the 150 m experimental feeder in the distance experiments.

(3) Finally, recruits may follow experienced foragers for *part* of the distance to the food source. This mechanism could explain why recruits arrive at the correct direction, but not at the correct distance. If they do not follow the forager the entire distance to the feeder, many may first encounter and choose the closest feeder. In our distance experiments, 61% of newcomers arrived at the 50 m control feeder (the closest feeder). Thus recruits do not appear to follow experienced foragers the entire distance to the food source.

Conclusions

Our results show that *Trigona carbonaria* recruits can search in the correct direction but evidently not at the correct distance for an advertised food source. In the scented direction experiments, significantly more newcomers arrived at the experimental feeder when it was scented and placed upwind of the nest and when it was unscented and conditions favored rapid recruitment levels (50 newcomers/hour). However significantly more newcomers failed to arrive at the experimental feeder in unscented direction trials with low recruitment levels (10 newcomers/hour). Thus the communication of food direction is weak or may not occur under conditions favoring slow recruitment (such as an abundance of natural food).

Newcomers apparently did not fly out and search at the correct distance from the nest. Instead, they generally preferred the closest feeder. These results suggest that newcomers orient to the scent of the food source. They may also orient to a pheromone deposited at the food source and follow experienced foragers for part of the distance to the food source.

Future research should assess the recruitment behaviors exhibited by foragers outside and inside the nest. Outside the nest, it will be particularly interesting to determine if newcomers can follow experienced foragers for part of the distance to the food site. This mechanism is often discussed (Lindauer & Kerr 1958; Kerr 1969), but no studies have provided strong proof that it exists.

Inside the nest, recruiting foragers in many stingless bee species such as *Nannotrigona testaceicornis* produce buzzing sounds and randomly oriented zig-zag runs that are merely excitatory and do not communicate location information (Kerr 1969). *T. carbonaria* may also exhibit such excitatory behavior since we were able to record vibrational sound pulses, apparently related to foraging, with a small accelerometer mounted on the nest entrance. We detected these vibrational pulses only during periods of high foraging flight activity when bees were not resting outside the nest entrance but flying directly inside the nest. Recruitment behavior inside the nest will consequently be the focus of a future study.

Finally, it is interesting to note that virtually all highly social bees, including honey bees, appear to incorporate communication features such as orientation to the food odor, orientation to a pheromone deposited at the food source, and random excitatory movements and sound inside the nest (von Frisch 1967; Michener 1974; Seeley 1998). These features possess varying importance, but their existence suggests that highly social bees have not discarded earlier innovations in the evolution of recruit-

ment communication systems. Such retention could arise from the advantages of exploiting multiple, redundant communication channels. However, *Trigona carbonaria*'s weak communication of direction and inability to communicate distance suggests that even mechanisms that imprecisely specify location can suffice for colony needs. For example, Jarau et al. (1998) have recently collected evidence that two Brazilian stingless bees, *Melipona quadrifasciata* and *Melipona scutellaris*, imprecisely communicate distance when the food source is close to the nest (<100 m). Thus simple communication mechanisms may also persist because they are effective and sufficiently accurate under most natural conditions. The reasons for this efficacy should be a focus of future research on the forces driving the evolution of recruitment communication.

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