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Pulsed mass recruitment by a stingless bee, *Trigona hyalinata*

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Research on bee communication has focused on the ability of the highly social bees, stingless bees (Hymenoptera, Apidae, Meliponini) and honeybees (Apidae, Apini), to communicate food location to nest-mates. Honeybees can communicate food location through the famous waggle dance. Stingless bees are closely related to honeybees and communicate food location through a variety of different mechanisms, many of which are poorly understood. We show that a stingless bee, *Trigona hyalinata*, uses a pulsed mass-recruitment system that is highly focused in time and space. Foragers produced an ephemeral, polarized, odour trail consisting of mandibular gland secretions. Surprisingly, the odour trail extended only a short distance away from the food source, instead of providing a complete trail between the nest and the food source (as has been described for other stingless bees). This abbreviated trail may represent an intermediate strategy between full-trail marking, found in some stingless bees, and odour marking of the food alone, found in stingless bees and honeybees.

Keywords: recruitment; stingless bee; foraging; polarized short odour trail

1. INTRODUCTION

Stingless bees live in competitive environments in which food resources are highly sought after, and they exploit these resources with strategies ranging from solitary foraging to the mass recruitment of nest-mates (Johnson 1980; Johnson & Hubbell 1987). Stingless bees employ a matching diversity of recruitment communication strategies, ranging from odour communication to the potential communication of resource location through sounds produced inside the nest (Lindauer & Kerr 1958; Esch *et al.* 1965; Biesmeijer *et al.* 1998; Nieh & Roubik 1998; Aguilar & Briceño 2002; Slaa *et al.* 2003). The aggressive defence and attack of good food sources is a key element in meliponine foraging competition (Roubik 1980, 1982), and is thought to play a significant role in the evolution of meliponine foraging strategies (Kerr 1960, 1969; Johnson 1974; Johnson & Hubbell 1974, 1987; Roubik 2002).

Several species of stingless bees such as *T. fuscipennis*, *T. silvestriana*, *T. williana* and *T. hyalinata* readily attack and displace conspecifics and interspecifics on rich food sources (Johnson & Hubbell 1974, 1975; Roubik 1980; Johnson 1981). *Trigona hyalinata* is one of the most aggressive of these species. It is found throughout South America, and lives in large colonies of up to 40 000 foragers. Moreover, its aggression is not limited to food sources. A *T. hyalinata* colony will attack stingless bee colonies up to 200 m away from its nest (P. Nogueira-Neto, personal communication). Roubik (1980) reported that *T. hyalinata* would attack and could successfully displace other stingless bee species and a small colony of Africanized honeybees from rich food sources. However, the recruitment mechanisms used by such aggressive foragers are poorly understood.

Odour orientation plays a major role in meliponine recruitment. Stingless bees can orient to floral and locale odours (Slaa *et al.* 1998) and can assist forager orientation by odour marking the resource alone (Nieh 1998; Aguilar & Sommeijer 2001; Jarau *et al.* 2002; Hrncir *et al.* 2003; Nieh *et al.* 2003) or odour marking the resource and using odour trails that extend from the resource to the nest (Lindauer & Kerr 1958; Kerr 1973; Johnson & Hubbell 1974; Hubbell & Johnson 1978; Schmidt *et al.* 2003). Meliponine odour trails consist of odour droplets placed every few metres to form a trail leading from the nest to the indicated resource and can be up to 900 m long (Kerr 1960). Odour trails are thought to provide additional guidance to groups of recruits led by an experienced forager (Lindauer & Kerr 1958; Kerr 1972, 1973; Kerr *et al.* 1981). However, the extent of these trails, the spatial distribution of odour droplets and the influence of such trails on forager orientation have not been clearly elucidated.

Our study therefore had two goals: (i) to determine the mechanisms underlying recruitment in *T. hyalinata*, and (ii) to determine the role of odour trails in the recruitment system of *T. hyalinata*.

2. MATERIAL AND METHODS

(a) *Measuring recruitment and the frequency of odour marking*

We conducted these experiments at the Fazenda Aretuzina (21°26.432′ S, 047°34.910′ W), in the state of São Paulo, Brazil, during the spring of 2001. To investigate the recruitment communication system of *T. hyalinata*, we trained individually marked foragers to a simulated dense flower patch (Johnson 1981), a grooved-plate feeder containing a rich 2.5 M scented

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sucrose solution (100 µl of anise extract per litre of solution, McCormick & Co. Inc.) located 146 m SW of the nest (method of von Frisch 1967). The control and experimental feeders were identical and contained the same quantities of scented 2.5 M sucrose solution. However, we immediately captured all bees landing on the control feeder to eliminate recruitment to the control feeder. We marked each visiting bee with an individual combination of paint marks on the thorax. We monitored the visiting foragers each 15 min and allowed only 10 individually marked foragers to feed. We captured all other foragers with aspirators and did not release them. Thus foragers were not multiply counted.

A newcomer is a forager from the subject colony who has not previously visited any feeder (Biesmeijer & de Vries 2001). To determine whether foragers visiting the feeder came from the subject colony and were motivated by recruiters to find the food source, we counted the number of newcomers arriving after we eliminated recruitment by capturing all foragers. We conducted three hour-long control trials on three separate days.

Stingless bees deposit odour trails by preferentially placing odour marks on prominent leaves elevated above the substrate. They will also odour mark leaves placed on an elevated rope, creating a trail with odour marks spaced along the rope, as they are on a natural substrate (Lindauer & Kerr 1958; Kerr *et al.* 1963). To study the odour trail, we therefore attached a 100 m rope leading from the feeder towards the nest and fastened leaves at 1 m intervals along the rope (method of Lindauer & Kerr 1960). We attached leaves at 1 m intervals to all ropes used in our experiments. This technique allows one to move stingless bee pheromone trails by shifting the location of the rope. Observers followed odour-marking bees and recorded mark locations to the nearest 0.5 m.

To analyse marking behaviour in detail, we digitally videotaped foragers depositing odour marks on a leaf attached to the feeder, and analysed the video (30 frames s^{-1}) on a Macintosh iBook computer with iMovie software.

(b) *Testing the attractiveness of odour marks deposited on the resource*

We tested the attractiveness of putative odour marks in a paired-feeder assay. We offered newcomers a choice between two identical clean feeders. Around each feeder, we placed a ring of filter paper: one paper that had been putatively marked by foragers for 60 min, and one that foragers had not contacted. We placed feeders 1 m to the right and to the left of the original feeding site and captured bees as soon as they landed. During odour bioassays, we immediately captured all bees as soon as they landed on a feeder and only counted individual choices made in the absence of other bees. We exchanged the control and experimental feeder positions at 1 min intervals to eliminate site bias (total trial time of 5 min) and discontinued the bioassays when the wind direction was not parallel to the feeder-to-nest axis and thus could have biased foragers to visit one feeder over the other. During the trials, such wind conditions occurred twice for intervals of *ca.* 15 min each.

(c) *Testing the attractiveness of the odour trail*

To test the attractiveness of the odour trail, we performed a V-shaped rope experiment with the leaf-bedecked ropes. We attached one end of a 50 m rope (the nest-proximal end) to a tripod 96 m from the nest. We attached the distal end of the rope to a feeder 146 m from the nest. The rope pointed directly towards the nest. In the odour-collection phase, we allowed foragers to odour-mark the rope for 30 min. In the test phase, we removed the original training feeder, sealed it inside a plastic bag, and set out two identical, clean feeders, 10 m to the left and right of the training location. We then moved the distal end of the marked rope to one of the clean feeders and attached an identical but *unmarked* rope to the other clean feeder. We attached the proximal ends of both ropes to the same tripod and thus formed a V-shaped rope array. We alternated the position of the marked rope from trial to trial.

(d) *The spatial distribution of odour marks*

To determine the spatial distribution of odour marks, we intersected two perpendicular crossed ropes at the training feeder. From the feeder, the ropes extended for 100 m in the direction of the nest, 20 m in the other three directions. Three observers recorded the location and sequence of all odour marks deposited on the ropes to an accuracy of 0.5 m.

(e) *Testing the polarity of the odour trail*

We tested newcomer orientation within the trail by providing a choice between the training feeder and an identical control feeder located within the trail but 20 m closer to the nest. The trail extended 27 m away from the feeder in the direction of the nest, as determined by the maximum extent of odour marking on the rope (see § 3).

(f) *Testing mandibular gland extracts*

Several stingless bee species use mandibular gland pheromone to odour-mark food sources and to create odour trails (Kerr *et al.* 1963; Blum *et al.* 1970). We observed *T. hyalinata* foragers appearing to odour-mark by briefly landing and rubbing their mandibles against the substrate. We therefore extracted and tested the attractiveness of *T. hyalinata* mandibular gland pheromone.

We prepared extracts by using plastic bags to carefully capture non-alarmed foragers leaving the feeder, chilling the bees, and dissecting out the mandibular glands. We crushed three glands in 1.5 ml of hexane (to standardize extract concentration), and stored 0.5 ml of the extract in a sealed centrifuge vial at −20 °C until the beginning of the bioassay, when we attached and opened the tube on the side of a feeder. Control vials contained 0.5 ml of hexane and were handled and stored in the same way, but did not contain mandibular gland pheromone.

During the collection and test phases, we used two clean forceps, one to handle the test filter paper and one to handle the control filter paper. We kept a supply of several clean glass feeders on hand. Once used, we washed the forceps and test feeders in a strong detergent, rinsing thoroughly with hot water followed by two washes of 95% ethanol. We air-dried all apparatus for at least 3 h before reuse. Even without washing, this time-interval is more than sufficient for any odour marks to completely evaporate (see figure 4). The experimenter wore disposable latex gloves during all feeder choice experiments and while washing glassware. After each trial, we discarded the gloves and all paper and plastic items used in the trial.

(g) *Statistical analyses*

We use the χ^2-test to determine the significance of the recruitment control trials. In two-feeder experiments, we calculate probabilities from a two-tailed binomial distribution with $p = q = 0.5$.

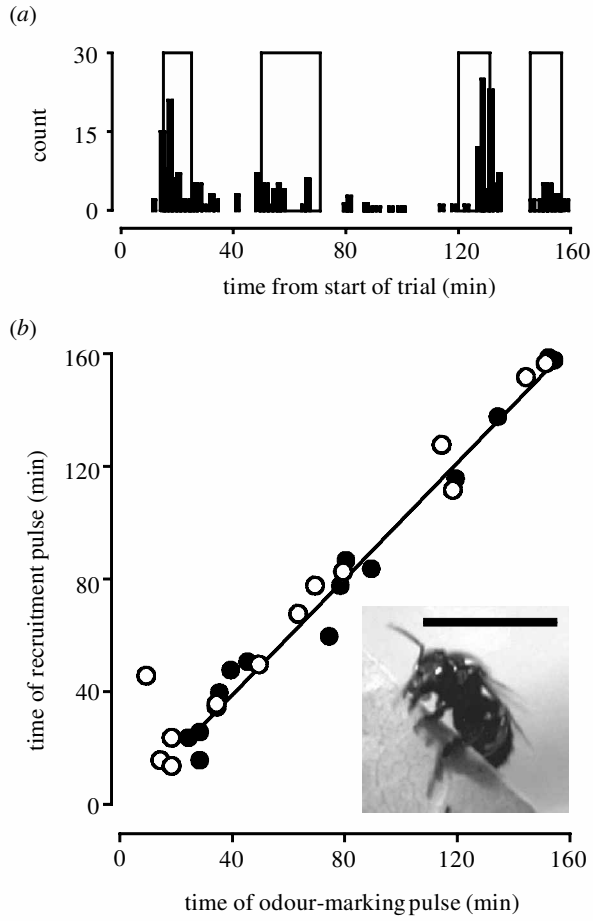

Figure 1. Temporal synchronization of recruitment and odour marking. (*a*) Recruitment occurs in pulses (trial 1, 10.00 start time, $n = 231$ newcomers). Black bars show the number of recruits. Open bars show intervals of forager odour marking. (*b*) Timing of major recruitment pulses is tightly linked to odour deposition. Start (open circles) and stop (filled circles) times of recruitment and odour-marking pulses are plotted. Data from five trials. Linear regression line shown: $r^2 = 0.98$, $p < 0.0001$. Scale bar, 5 mm.

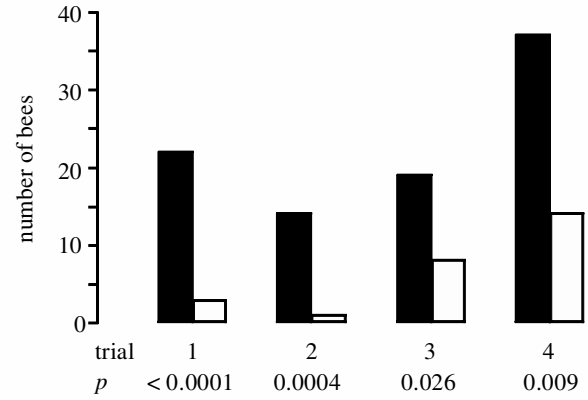

Figure 2. Attractiveness of odours deposited by foragers on the feeder. Feeder choice experiment. Black bars, previously visited feeder; open bars, clean feeder.

3. RESULTS

(a) *Measuring recruitment and observing odour marking*

Foragers recruited in large pulses in which over 100 newcomers could arrive within a 15–20 min interval (five trials, 3 h each trial; figure 1*a*). No newcomers arrived once the marked foragers were captured during three hour-long control trials conducted over 3 days, although a significantly greater number of newcomers had arrived in an equal time-period immediately before each forager-removal trial (three trials, $\chi^2 = 8$, 1 d.f., $p \leqslant 0.005$). Newcomer arrivals therefore decreased significantly once we removed the foragers at the feeder. Based upon these results, we counted unmarked foragers as newcomers from our subject colony.

The largest recruitment burst was 201 newcomers in 11 min. In addition, foragers landed and deposited putative odour marks on the feeder and rope during large recruitment bursts. The start and stop times of major recruitment pulses (more than one newcomer per min) are highly correlated with the start and stop times of the putative odour marking (figure 1*b*). Foragers landed only on the rope and feeder. Foragers did not land on any other substrate. The putative odour-marking behaviour consisted of a forager landing for 1.35 ± 0.66 s (s.d.) while rubbing her mandibles for 0.66 ± 0.64 s against the substrate. In 57% of landings, foragers also rubbed their tongues against the substrate for 0.13 ± 0.06 s ($n = 32$ observations).

(b) *Testing the attractiveness of odour marks deposited on the resource*

Significantly more newcomers chose the feeder with the forager-marked filter paper in all trials (figure 2; two-tailed binomial probability, pooled data, two-tailed binomial probability, $p \ll 0.000\,01$, four trials, $n = 118$ newcomers). Thus foragers evidently deposited attractive odour marks on the feeder.

(c) *Testing the attractiveness of the short odour trail*

We next tested the attractiveness of odour marks on the rope with the V-shaped rope experiment. A significant majority of newcomers (61–94%) chose the feeder linked to the forager-marked rope over the feeder linked to the unmarked rope within the first 15 min (pooled data, two-tailed binomial probability, $p \ll 0.000\,01$, five trials, $n = 244$ newcomers). Thus forager-deposited odour marks on the rope could also guide newcomers to a feeder.

(d) *The spatial distribution of odour marks*

Unlike previous descriptions of stingless bee recruitment trails, these odour marks did not form a trail leading *the entire distance* from the nest to the food source (Lindauer & Kerr 1960). Instead, the marks extended only a short distance from the food source. We therefore call this formation a short odour trail. When we centred crossed ropes on the feeder, foragers laid most marks in the nest direction and occasionally deposited multiple marks during a single marking run (figure 3*a*,*b*). The marks formed a decreasing concentration gradient extending a maximum of 27 m from the feeder (three trials; figure 3*c*).

(e) *Testing the polarity of the short odour trail*

Because the concentration gradient polarizes the short odour trail, it may allow newcomers to determine the cor-

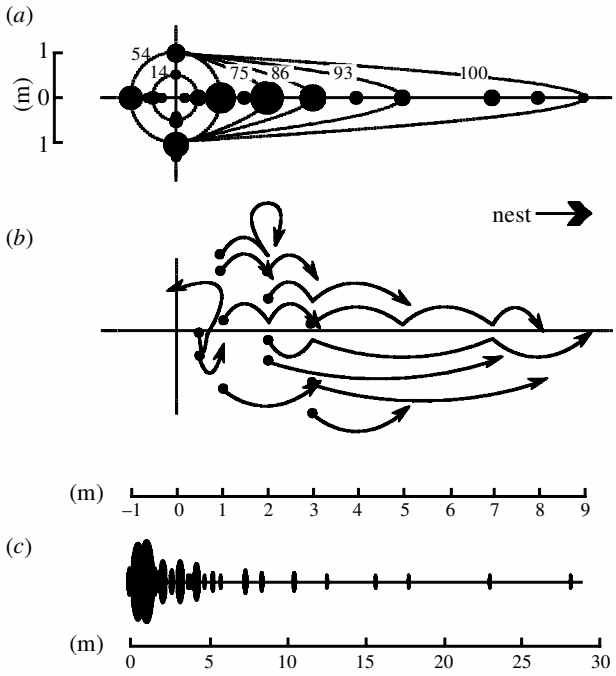

Figure 3. Short, polarized odour trail created by recruiting foragers. (*a*) Crossed-ropes experiment. Odour marks ($n = 81$) are most concentrated at the food source (0 m), and decrease in number in the direction of the nest. Area of circles corresponds to the number of marks. Isoclines give the percentage of marks within set distances. (*b*) Deposition sequence of multiple marks during individual marking runs on crossed ropes. Initial mark shown as a circle. Arrows indicate subsequent marks. Paths vertically displaced to show the marking pattern better. (*c*) Maximum extent of short odour trail ($n = 103$ marks).

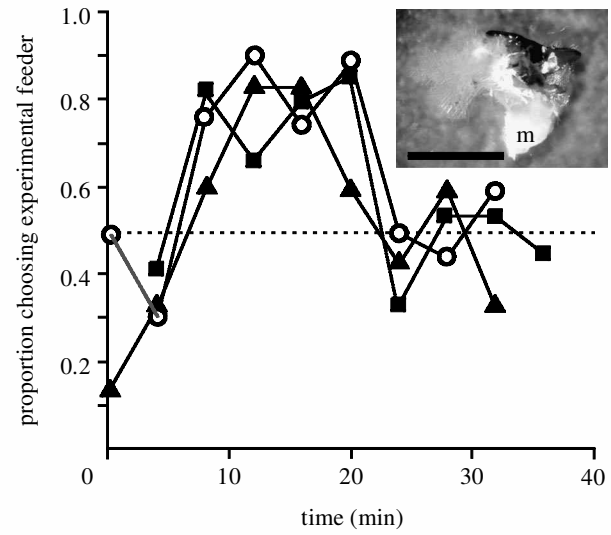

Figure 4. Mandibular gland extracts attract foragers to land and to begin feeding from 7 to 20 min after deposition. Inset shows dissected mandibular gland (m) attached to a mandible (scale bar, 1 mm). The graph shows the results of three trials.

rect endpoint. Significantly more newcomers chose the training feeder in all polarity-test trials (six trials, pooled data: $p \ll 0.000\,01$, $n = 75$ newcomers). Thus newcomers preferred to land in the region of highest pheromone mark concentration.

(f) *Testing mandibular gland extracts*

Using the paired-feeder assay, we presented the equivalent of one mandibular gland in hexane at the experimental feeder and a hexane blank at the control feeder. From 0 to 8 min, newcomers attacked the extract vial by hovering and biting the vial lip. Newcomers did not land and feed until after 8 min had passed. From 8 to 20 min, they showed a strong preference for landing and feeding on the experimental feeder over the control feeder (60–91% on the experimental, three trials, two-tailed binomial probability, $p = 0.0003$, $n = 273$ newcomers; figure 4). Attraction to the mandibular gland extract thus persisted for 12 min, corresponding well to the 15 min period in which the naturally deposited short odour trail influenced newcomer choice.

4. DISCUSSION

Our experiments reveal that *T. hyalinata* foragers can recruit a large number of nest-mates in recruitment pulses that are highly focused in time and space (figure 1*a*): 10 foragers recruited up to 201 newcomers in 11 min. Because recruiters and newcomers arrived in large groups, recruiters may have guided recruits from the nest and assisted final recruit orientation with a short, polarized odour trail. This short odour trail extended only a short distance from the food source instead of providing a complete trail between the nest and the food source. The stingless bee *Scaptotrigona postica* also deposits a polarized odour trail (Kerr *et al.* 1963). However, most previously reported stingless bee odour trails have extended from the nest to the food source (Lindauer & Kerr 1958; Kerr *et al.* 1963, 1981). Kerr & Rocha (1988) reported potential odour-marking behaviour that may have created a short odour trail in *Melipona rufiventris* and *M. compressipes*, but it is unclear whether the potential marks were attractive to nest-mates.

Mandibular gland volatiles serve as alarm odours in honeybees and many stingless bee species (Cruz-Landim 1967; Collins *et al.* 1989). *Trigona hyalinata* recruiters evidently use mandibular gland secretions to create the short odour trail to guide nest-mates. Chemical analysis of the odour marks is necessary to confirm their identity, but the deposition behaviour is characteristic of stingless bee mandibular gland marking, and mandibular gland extracts attracted foragers and exhibited a similar decay time to natural odour marks. Mandibular gland pheromone may also release an aggressive response in *T. hyalinata*, as it does in other highly social bees (Cruz-Landim 1967; Williams 1982; Collins *et al.* 1989). *Trigona hyalinata* is known to be an aggressive species that attacks and displaces other species at food sources (Roubik 1980). Recruited nest-mates were drawn to the highest concentration of odour marks, and thus mandibular gland pheromone could enable foragers to draw in reinforcements precisely where they are most needed to take over a rich food source.

Food-source competition may be an important factor in stingless bee evolution (Johnson 1974; Johnson & Hubbell 1974, 1987; Hubbell & Johnson 1978; Slaa *et al.* 1997). Several stingless bee species are reported to forage

aggressively, and elements of the pulsed mass-recruitment system—mandibular gland marking of resources, massive recruitment and aggressive attacks at and the defence of rich resources—are found to varying degrees in the Meliponini (Kerr *et al.* 1963; Blum *et al.* 1970; Roubik 1980). Some aggressive species appear to specialize in discovering and exploiting good food sources found by other bees (Johnson 1974; Hubbell & Johnson 1978; Nagamitsu & Inoue 1997). Thus, it is possible to view the precise spatial and temporal communication offered by the ephemeral, short odour trail in an alternative light: crypsis. An extended, consistently renewed odour trail offers a more conspicuous target than a temporary, short odour trail (Bradbury & Vehrencamp 1988; Hölldobler & Wilson 1990). The work of Kerr *et al.* (1963) suggests that some meliponine species, *Scaptotrigona postica* and *S. xanthotricha*, can detect and use interspecific odour trails. Thus an abbreviated trail may be less conspicuous to foraging competitors, and may represent an intermediate strategy between point-source marking of the resource alone and full-trail marking from the resource to the nest.

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