



Collective foraging in a stingless bee: dependence on food profitability and sequence of discovery

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We examined the ability of *Trigona recursa*, a scent trail-laying stingless bee, to allocate foragers to the more profitable of two food sources. Imbibing time and imbibed volume of individuals were the same at feeders containing 20% or 40% w/w (weight in weight) sugar solution. However, sugar intake rate and sugar per crop load were significantly higher for the 40% solution, which was therefore more profitable. Collective foraging of two colonies was observed without interference with the recruitment process. One bee was trained to a 20% food source and another at the same time to a 40% source. Recruitment to both food sources started simultaneously. In all trials the majority of recruits landed at the 40% food source. This cannot be the result of bees comparing the two sugar concentrations because less than 1% of the recruits landed at both feeders. When we offered the 20% food source 90 min before the 40% source, the newcomers at the 40% food source never outnumbered the newcomers at the 20% source. Significantly more recruits landed at the less profitable food source. This is likely to be caused by a positive feedback resulting from the large number of bees that had already exploited the poor source and reinforced the scent trail. New recruits presumably selected the more intensively marked trail, neglecting the new and weakly marked one that would lead them to the richer food.

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Studies of recruitment in social insects have examined both the signals emitted and the cues received by individuals and the collective response of the colony to the recruitment communication (von Frisch 1965; Hölldobler & Wilson 1990; Seeley 1995). The majority of studies on the recruitment behaviour of stingless bees, however, have focused on the signals and cues of the individual recruiter (reviewed in Nieh 2004). Little work has been done on the collective response of the colony. Distinctive differences in collective foraging patterns between species have been found and these are believed to contribute to the coexistence of many species of stingless bees in a given habitat (Hubbel & Johnson 1978; Jarau et al. 2003).

In stingless bees, both the signals emitted by the recruiters and the resulting foraging activity of the entire

colony is affected by the profitability of the food source (Biesmeijer & Ermers 1999; Aguilar & Briceño 2002; Nieh et al. 2003; Hrncir et al. 2004). As one would expect, more nestmates are recruited to food sources of high sugar water concentrations than to ones of lower concentrations (Biesmeijer & Ermers 1999). Similarly, honeybees, *Apis mellifera*, focus their efforts on the most profitable food sources, gauging profitability by both the sugar concentration and the flow rate of the solution (von Frisch 1965; Núñez 1966; Seeley 1995; Dyer 2002). Sugar uptake rate (mg/s) and sugar mass (mg) carried by the forager are taken as measures of energy intake (Farina & Núñez 1991).

The importance of food profitability for recruitment in scent trail-laying stingless bees has not yet been studied. Many species of stingless bees, such as *Trigona recursa*, effectively and very precisely guide their nestmates by means of a scent trail to the food source (Lindauer & Kerr 1958; Kerr et al. 1963; Jarau et al. 2003, 2004; Schmidt et al. 2003; Sánchez et al. 2004; Nieh et al. 2004). In *T. recursa*, scent marks are typically deposited soon after the discovery of a food source (Jarau et al. 2004). First the forager deposits scent marks directly at

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the food source, then, on her way back to the nest, she lands regularly to deposit further marks on twigs and leaves. The pheromones originate from the labial glands and strongly attract nestmates searching for food (Jarau et al. 2004). The recruiting forager then enters the nest and displays intranidal recruitment behaviour such as jostling contacts, trophallaxis and vibrational signals, to stimulate other bees to leave the nest to search for food (Lindauer & Kerr 1958; Esch 1967; Schmidt et al. 2006). Upon leaving the nest, the recruited nestmates follow the scent trail towards the food source. However, the effect of food profitability on the recruitment pattern in scent trail-laying stingless bees is not yet known.

Studies on scent trail-laying ants have shown that an increased allocation of the colony's foraging force to the more profitable of two food sources depends on the simultaneous discovery of both sources (Beckers et al. 1990; Sumpter & Beekman 2003). Ant colonies do not reallocate the workforce to a newly discovered richer food source while recruitment to a less profitable food source is still going on. Independent of food quality, the outcome of recruitment correlates with the number of recruits already exploiting a food source because an increasing number of foragers increasingly reinforce the scent trail (Pasteels et al. 1987; Goss et al. 1989; Beckers et al. 1990, 1992, 1993; Edelstein-Keshet et al. 1995; Nicolis & Deneubourg 1999; Sumpter & Beekman 2003; Sumpter & Pratt 2003).

We investigated whether the scent trail of a stingless bee affects the recruitment pattern, as it does in ants. Specifically, we asked whether a colony of *T. recursa* exploits a highly profitable food source more intensively than a simultaneously offered less profitable food source and whether *T. recursa* reallocates its workforce to a highly profitable new food source while recruitment to a less profitable one is still going on.

METHODS

All experiments were conducted on the campus of the University of São Paulo, Brazil, in Ribeirão Preto during September and October 2004. We studied two colonies (A and B) of *T. recursa* living naturally on the campus in subterranean nests. The nests were approximately 900 m apart. The foragers of the two colonies were marked with different colours upon their first arrival at a feeding station. Bees of one colony were never found at the nest entrance or at the feeders of the other colony. We found no other nests of this species in the area of our experiments.

Measuring Food Intake

The food and energy intake at different sugar water concentrations were measured for 10 different bees of colony B for each sugar water concentration (ambient temperature 28.8–33.1°C). We trained the bees to go to a feeding site, 30 m from the nest, where they were captured and marked with two coloured dots of paint on their thorax. Subsequently, one of them was released and allowed to fly back to her nest. Upon her return to the

feeding site, we put 20 µl of sugar water (Sigma Microcaps, 20 µl) with a concentration of either 20% or 40% weight in weight (w/w) onto a Plexiglas disc (Hrncir et al. 2004). We used a digital stopwatch to record how long the bee spent imbibing the sugar water (± 0.1 s). We removed sugar water left over by the bee, with a 20-µl microcapillary, immediately after the bee's departure to minimize evaporative losses. From the imbibing time (s) and the imbibed crop load (µl; crop load = $20 \mu\text{l} - x \mu\text{l}_{\text{remaining sugar water}}$), we calculated the solution intake rate (µl/s), the sugar intake rate (mg/s) and the total amount of sugar per crop load (mg). Upon her second return to the feeder, the same bee was captured and kept in a separate container. Then another of the bees originally captured at the feeder was released and the procedure repeated. We observed 20 bees in this way, i.e. 10 bees for each concentration. The sugar water was unscented in all cases and prepared with unrefined cane sugar (99.8% sucrose, 0.1% glucose and fructose, 0.1% mineral salts). Its concentration was measured with a field refractometer (Krüss Optronic HR 25/800). A 20% w/w sugar water concentration corresponds to a molarity of 0.63 M and a 40% w/w to 1.38 M (Weast et al. 1989).

Training Procedure

We first trained foragers to feed at an artificial feeder, an inverted glass vial on a grooved plate (Jarau et al. 2003), which contained sugar water at a concentration of 13% w/w and was mounted on a tripod 40 cm above the ground and 1 m from the nest entrance. The bees visited this feeding site but never recruited nestmates to it. We applied the Françon method to train a forager to go to the site of the experiment (Françon 1938; Kerr et al. 1963). A bee captured in an empty glass vial at the training feeder was carried to the new feeding site 30 m from the nest. There the inverted vial with the bee was put on to the new training feeder (40 cm above the ground, 13% sugar solution) and the bee was released after food uptake. The bee returned to the new feeding site within 3–8 min.

Simultaneous Discovery of Two Food Sources

To find out whether two food sources of different profitability are exploited by different numbers of recruits, we trained one forager to feed at a feeding site 30 m from the nest in one direction and a second forager of the same colony to feed at another feeder 30 m from the nest in another direction (Fig. 1a). Six trials were conducted in this way. We marked the foragers individually with two coloured dots on their thorax. The plastic paint used did not affect the behaviour of the bees (Jarau et al. 2003), which were allowed to feed three to four times at the 13% sugar water solution at the newly learned feeding site.

We then presented sugar water with altered concentrations at each site in fresh alcohol-cleaned feeding dishes. The foragers landed at the new feeder and were retained there under an inverted glass vial where they could taste the new sugar water solution (20% or 40%). We

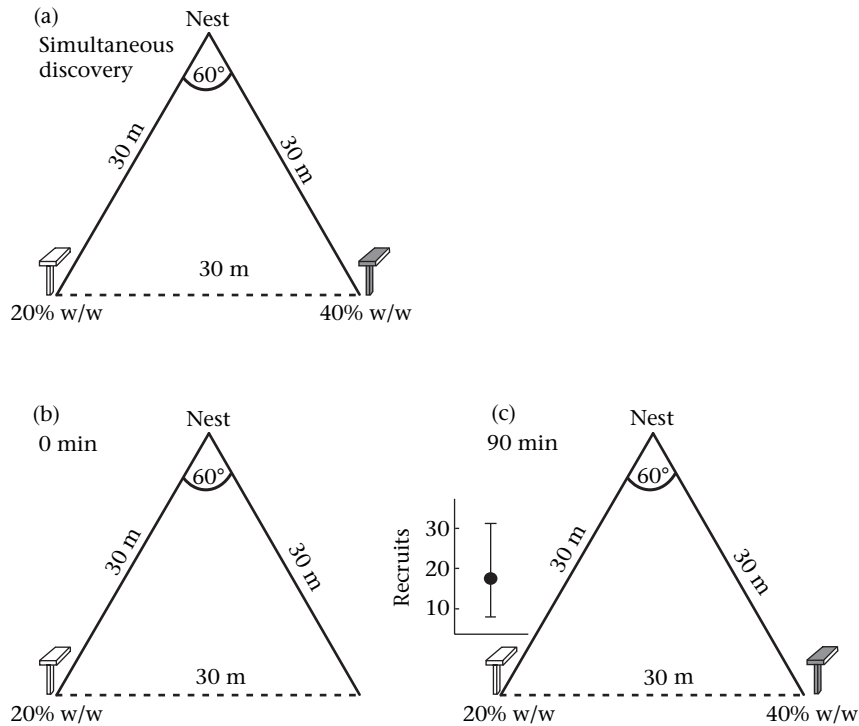


Figure 1. Experimental set-up. (a) Simultaneous discovery of two food sources. One forager was trained to the 20% and one to the 40% (weight in weight, w/w) food source. (b) Prior discovery of the less profitable food source: situation at the start of the trial when one forager was trained to feed at the 20% food source. (c) Situation 90 min later when one forager started to feed at the 40% food source. Inset in (c) shows median number of recruits at the less profitable food source after 90 min; vertical lines indicate first and third quartiles.

synchronized the start of recruitment to the two food sources (start of the trial) by releasing the foragers simultaneously at both feeding sites. During the subsequent 150 min every newly arriving bee was marked with a coloured dot on her thorax and her time of arrival was recorded. Jarau et al. (2003) found that 150 min was the maximum time span after which all available recruits (100%) had found an artificial feeding site 25 m from the nest. We did not interfere with the recruitment process by collecting newcomers, but allowed every newly arriving bee to collect food and recruit ad libitum.

We used different colours to mark bees according to different feeding sites and different days, so we could distinguish the first forager from the recruited bees at each feeding site and from experienced foragers. We avoided inspector bees spontaneously revisiting a known feeding site, or reactivated foragers revisiting a known feeding site after having received recruitment signals (Biesmeijer & de Vries 2001), by using new locations of the feeding sites in consecutive trials.

Prior Discovery of Less Profitable Food Source

To find out whether the workforce of *T. recursa* keeps to a feeding site discovered prior to another one, we offered the less profitable food source earlier than the highly profitable one. The number of trials in this test series was again six. One bee was trained to feed at a feeding site 30 m from the nest and marked with two colours (Fig. 1b). A trial started when the bee first took up 20% w/w sugar water

from the fresh alcohol-cleaned feeder. During the next 90 min, we marked every newly arriving bee with one coloured dot on her thorax and recorded her arrival time. Then, 90 min after having first fed at the 20% food source, the bees were offered the 40% food source at a distance of 30 m from both the 20% food source and the nest (Fig. 1c). The first forager at the 40% source was obtained from the training feeder close to the nest (13% sugar water, offered for 5–10 min until one bee was captured and trained to feed at the new feeding site) and was marked with two coloured dots. Again we recorded the time of arrival of every newcomer, which was marked with one coloured dot (differing from the colour used at the 20% food source and from previous trials). All trials ended after 180 min. In this way, equal periods could be compared for the two different situations with the 20% food source only and with both the 20% and the 40% food source.

Statistical Analyses

For data analyses, we used SigmaStat 3.1 (Systat Software Inc., Erkrath, Germany) and SPSS 11.0 (SPSS Inc., Chicago, IL, U.S.A.) software. Each test series ('simultaneous discovery experiment' and 'prior discovery experiment') consisted of six individual trials (total number of bees = 876). In cases where the Kolmogorov–Smirnov test (for normality) and the Levene median test (for equal variance) passed (NS), the data are presented as mean percentages \pm SD and parametric tests were applied (*t* test to compare two samples, one-way ANOVA to

compare more than two samples). When the Kolmogorov–Smirnov test or the Levene median test indicated non-normal distribution or nonequal variance ($P < 0.05$) the median percentage (first quartile/third quartile) is given and nonparametric tests were applied (Mann–Whitney U test and Kruskal–Wallis test, respectively; Sokal & Rohlf 1995). Colony A was used for two and colony B for four trials per test series. All analysed parameters were compared between colonies A and B to test whether their differences were due to random sampling variability. We found no significant differences between any of them (t tests and Mann–Whitney U tests: NS), so we pooled the data from the two colonies. All reported P values are two tailed.

RESULTS

Food Intake and Food Profitability

When feeding on 20% w/w sugar water (offered independently from the higher concentration) *T. recursa* foragers spent a median of 20.9 s (19.8/22.0) to imbibe 6.4 μ l (5.9/7.4) of sugar solution (Fig. 2a, b). Values did not differ significantly from these when the bees fed at 40% w/w sugar water (offered independently from the lower concentration; Fig. 2a, b). Imbibing time and imbibed volume at the higher concentration were 21.5 s (21.0/23.8) and 6.8 μ l (6.3/7.3) (t test: time: $t_{18} = 1.825$,

$P = 0.09$; Mann–Whitney U test: volume: $U = 39$, $N_1 = N_2 = 10$, $P = 0.4$). Accordingly, the solution intake rate was the same for both concentrations (0.311 \pm 0.04 μ l/s at 20%, 0.309 \pm 0.04 μ l/s at 40%; t test: $t_{18} = 0.111$, $P = 0.9$). However, the sugar intake rates differed significantly between 20% (0.065 mg/s [0.06/0.07]) and 40% w/w sugar water solutions (0.15 mg/s [0.13/0.16]; Mann–Whitney U test: $U = 0$, $N_1 = N_2 = 10$, $P < 0.001$; Fig. 2c). Similarly, the sugar carried per crop load was significantly less for the 20% sugar solution (1.8 mg [1.27/1.6]) than for the 40% solution (3.22 mg [2.98/3.45]; $U = 0$, $N_1 = N_2 = 10$, $P < 0.001$; Fig. 2d). Thus, the 40% food source was significantly more profitable for the bees than the 20% food source.

Food Sources of Different Profitabilities

In the simultaneous discovery experiment, we counted 459 bees (263 from colony A, 196 from colony B, 76.5 \pm 52.4 bees per trial) at the feeders. In the prior discovery experiment, 417 bees came to the feeders (139 from colony A, 278 from colony B, 69.5 \pm 67.5 bees per trial). There was no significant difference in any of the analysed parameters between the two colonies (t tests and Mann–Whitney U tests: NS). Only a minor fraction of the bees visiting the feeders were experienced bees that had learned to feed at the artificial food source in an earlier trial. During both the simultaneous discovery

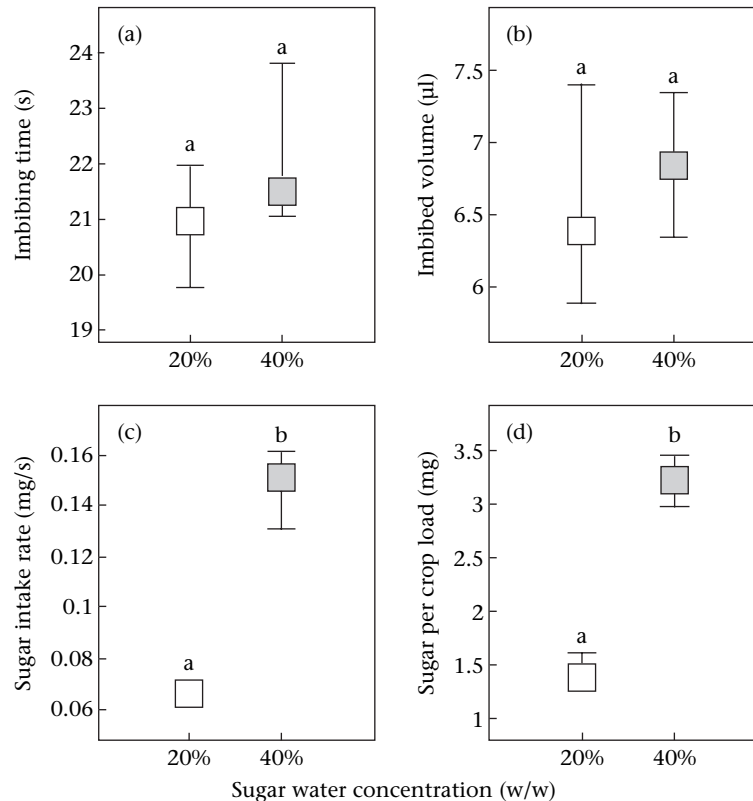


Figure 2. Food intake by *Trigona recursa* at two sugar water concentrations (weight in weight, w/w) each offered individually. (a) Time spent imbibing, (b) amount imbibed, (c) intake rate and (d) amount of sugar per crop load. Data are represented as medians, with vertical lines indicating first and third quartiles. Different letters mark significant differences ($P < 0.05$) between the groups.

experiment and the prior discovery experiment a median of only three bees carried the colour marks of a previous trial. In addition, the distribution of these bees at the feeders was identical to that of the newly recruited bees (Mann–Whitney U tests: simultaneous discovery: $U = 13$, $N_1 = N_2 = 6$, $P = 0.5$; prior discovery: $U = 16.5$, $N_1 = N_2 = 6$, $P = 0.8$). We therefore included the small number of experienced bees in our data.

Simultaneous discovery

When both food sources were offered simultaneously the number of recruits at the 40% food source (63.5 [21/81]) at the end of the trial was significantly higher than that at the 20% food source (12 [4/16]; Mann–Whitney U test: $U = 2$, $N_1 = N_2 = 6$, $P < 0.01$). When expressed as a percentage of the number of bees at both feeders after 150 min (100%) the 40% food source was clearly exploited more (84.9% [82/89.5]) than would be expected for a random distribution (50:50%; one sample t test: $t_5 = 17.2$, $P < 0.001$; Fig. 3a). The colony's choice did not result from the decision of each individual forager to feed at the more or the less profitable food source. In the majority of trials no bee appeared at both feeding sites. On average only 0.7 ± 0.8 bees tasted and potentially compared the sugar water at both feeders.

Prior discovery

When the less profitable food source was offered 90 min prior to the more profitable one, the numbers of recruits at the feeding sites did not differ significantly from each other (at 20%: $N = 50.8 \pm 41$; at 40%: $N = 18.7 \pm 25$; t test: $t_{10} = 1.573$, $P = 0.14$). However, between 90 and 180 min more recruits arrived at the 20% food source than at the 40% food source in all six trials when both feeders were offered. We therefore compared the percentage of recruits exploiting the 20% feeder from minutes 0–90 of the trial with that at minutes 90–180 (when both feeders were offered) and with that of the bees visiting the 40% feeder. Significantly, fewer recruits collected at the 40% than at the 20% food source (40%: $20.8 \pm 16.9\%$; 20%: $42.9 \pm 7.9\%$) over the same time span of

90 min before the end of the trial (ANOVA: $F_{2,16} = 4.1$, Tukey's pairwise comparison, $P < 0.05$; Fig. 3b). Thus, the more profitable food source was exploited by fewer recruits when there was an ongoing recruitment to the less profitable food source. Again, this distribution was not due to the decision of individual bees, as hardly any of them examined both feeding sites (median of 0 [0/1] bees).

Time course of exploitation

When both food sources were offered simultaneously, the percentage of recruits at the 40% sugar concentration was significantly higher than expected from a random distribution (50:50%) from the 35th min of the trial onwards (one sample t tests: $t_5 = 3.02$ – 17.2 , $P < 0.05$; Fig. 4a). However, the discovery of the 40% solution 90 min after the discovery of the 20% solution caused its underexploitation (Fig. 4b). In this case, the percentage of recruits at the 40% feeding site was significantly smaller than expected for a random distribution throughout the trial (one sample t tests: $t_5 = 2.7$ – 14.1 , $P < 0.05$).

The cascade of recruitment did not start significantly earlier at one of the two food sources. The times elapsed until the first forager returned to the feeding site after the first food uptake did not differ significantly between sugar water concentrations when they were offered simultaneously at both sites (at 20%: 2.5 ± 0.8 min; at 40%: 3.7 ± 2.2 min) nor when the 20% food source was offered before the 40% food source (at 20%: 4.2 ± 1.4 min; at 40%: 3.5 ± 2.1 min; t test: simultaneous discovery: $t_{10} = 1.234$, $P = 0.24$; prior discovery: $t_{10} = 0.663$, $P = 0.52$). Similarly, the time of arrival of the first recruited bee at the feeder was the same in both test series (simultaneous discovery: $t_{10} = 0.898$, $P = 0.4$; prior discovery: $t_{10} = 0.486$, $P = 0.6$). During the simultaneous discovery experiment, the first recruits arrived after 29.8 ± 23.3 min at the 20% feeder and after 20.0 ± 13.2 min at the 40% feeder. When the 20% feeder was offered before the 40% feeder the first recruits landed there after 15.5 ± 11.9 min and at the 40% feeder 19.2 ± 13.3 min after its introduction.

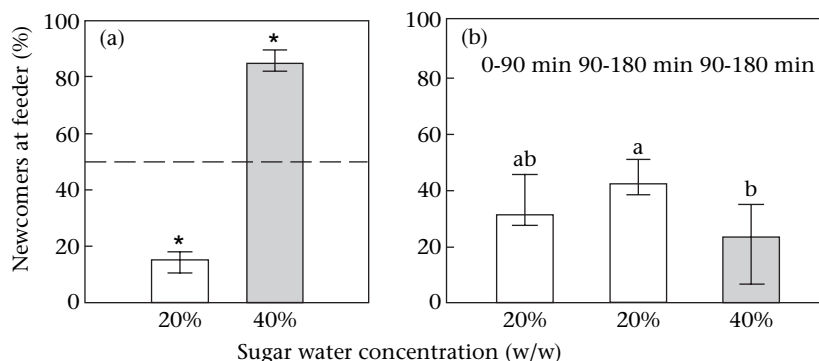


Figure 3. Recruitment of *Trigona recursa* to food sources of different profitability (20% and 40% weight in weight, w/w, concentration). The bars represent medians, with the first and third quartiles indicated by vertical lines. 100% = total number of recruits per trial. (a) Simultaneous discovery of both food sources. Dashed line indicates a random distribution and asterisks represent significant differences ($P < 0.05$) from it. (b) Prior discovery of the less profitable food source. Different letters mark significant differences ($P < 0.05$) between the percentages of newcomers at the feeders.

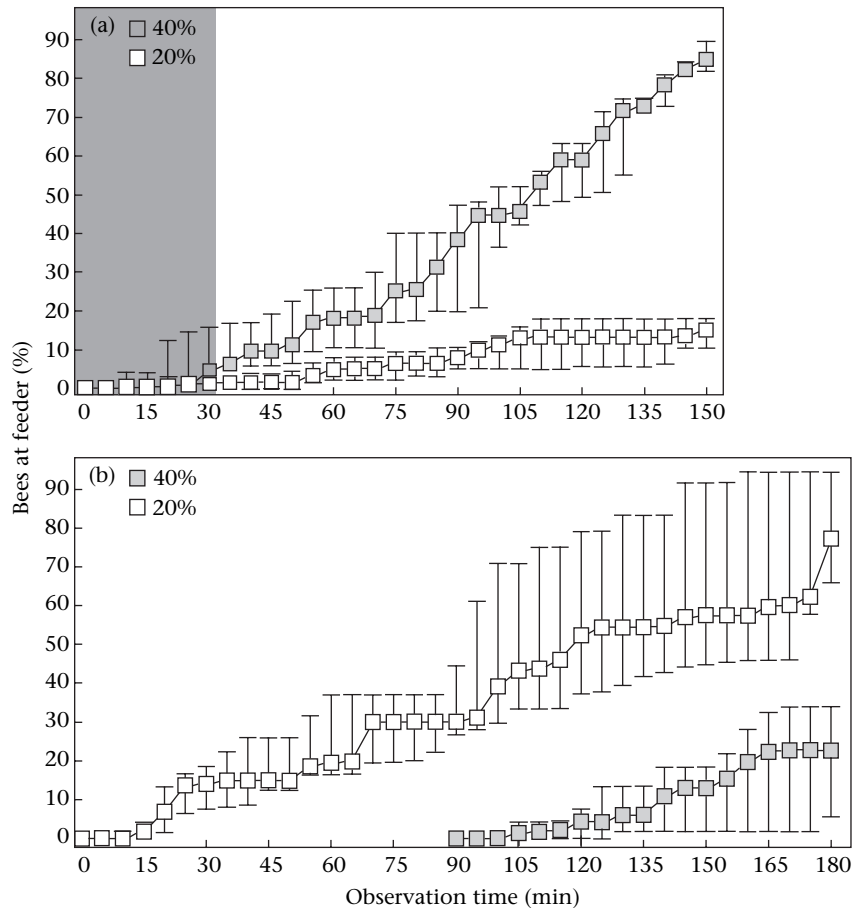


Figure 4. (a) Simultaneous discovery of two food sources of different profitability (20% and 40% weight in weight, w/w, concentration). 100% = number of bees at both feeders at the end of the trial. Symbols represent median percentages per 5-min interval, with the first and third quartiles indicated by vertical lines. The shaded area represents the time span with equally intensive exploitation of both food sources. (b) Prior discovery of the less profitable food source.

DISCUSSION

We found that in *T. recursa* the exploitation of food sources of different profitability depended on the sequence of their discovery. A colony exploited the more profitable food source more intensively than the less profitable one when they were discovered simultaneously. However, when the more profitable food source was discovered later, the bees kept to the food source discovered first despite its lower concentration.

Collective Foraging Patterns

In *T. recursa*, as in other social hymenopterans, the selection of one of several food sources was the result of feedback cascades on the level of the entire colony and the underlying decision-making process was decentralized, with no comparison between alternative food sources by the individuals of the colony (honeybees: Seeley et al. 1991; Seeley 1995; Dyer 2002; stingless bees: Biesmeijer & Ermers 1999; ants: Pasteels et al. 1987; Goss et al. 1989; Beckers et al. 1992). The particular concept of self-organization explains how complex collective behaviours emerge from interactions among individuals

that show simple behaviours. Self-organization can be defined as a set of dynamic mechanisms whereby structure appears at the colony level from interactions among individuals that act on purely local information (Bonabeau et al. 1997). Structure emerges as a result of basic ingredients of self-organization: (1) positive feedback (amplification such as recruitment and reinforcement); (2) negative feedback (abandonment, saturation, exhaustion); and (3) multiple interactions between individuals (Bonabeau et al. 1997).

Many studies on social hymenopterans have shown that self-organization is essential for creating a particular foraging pattern which depends on the mechanisms and communication used during foraging. So far, the mechanisms used by scent trail-laying colonies have been studied mostly in ants (e.g. Beckers et al. 1990, 1993; Sumpter & Beekman 2003).

(1) Positive feedback. In cases where a pheromone trail guides recruited individuals to the food source, the recruits again add their own pheromone on to the trail when returning to the nest. Hence, recruitment and reinforcement of the scent trail enhance the probability of other ants following this trail. In experiments where scent trail-laying ants discovered several food sources

simultaneously, the more profitable food source was exploited by more nestmates than the less profitable one (Beckers et al. 1990, 1993; Sumpter & Beekman 2003). The same was true for the scent trail-laying stingless bee *T. recursa* in our simultaneous discovery experiment. In ants the positive feedback arises from individuals adjusting scent trail marking according to food profitability (Breed et al. 1987; Pasteels et al. 1987; Fewell et al. 1992; Beckers et al. 1993; Mercier & Lenoir 1999). The autocatalytic nature of recruitment amplifies even small differences in recruitment activity. The stronger the scent trail, the larger the number of recruits choosing and reinforcing it (Breed et al. 1987; Pasteels et al. 1987; Beckers et al. 1990, 1993; Mercier & Lenoir 1999; Sumpter & Beekman 2003).

In our study we could not measure the amount of scent marking by *T. recursa*. We observed in some cases that the first scent mark was deposited earlier at the more profitable food source than at the other one, but the effect was not significant. The outcome of the recruitment activity (Fig. 4a) nevertheless showed that recruitment to the more profitable food source happened at a faster rate than for the less profitable food source. Apparently, a positive feedback amplified small initial differences to guide the large majority of recruits along the scent trail leading to the more profitable food source.

The remarkable finding that both ants (Beckers et al. 1990) and *T. recursa* (Figs 3b, 4b) stayed with the less profitable food source when it was introduced some time before the more profitable one can be explained by the same feedback mechanism. A large number of individuals already exploiting the poor source continuously reinforce the corresponding scent trail and new recruits are more likely to select the more intensively marked of the two trails. Owing to the prior discovery of the less profitable food source, this scent trail was already strong enough to attract more recruits than the scent trail to the more profitable food source offered only 90 min before the end of the trial. Therefore, the use of chemical trails during foraging limits the ability of both ants and stingless bees to reallocate their forager force quickly to newly discovered food sources.

(2) Negative feedback. Because we excluded both depletion and changes in the profitability of a given food source, we did not expect individual bees to abandon the food source in our study. However, in another set of experiments, foragers of *Scaptotrigona* aff. *depilis*, another scent trail-laying stingless bee, never abandoned the food source when confronted with decreasing food profitability. The foragers merely reduced their recruitment activity and recruitment stopped when food profitability was low (Schmidt et al. 2006).

(3) Multiple interactions between individuals. Self-organization in scent trail-laying species (ants as well as stingless bees) relies on the passing on of information not just to one but to many other recruits. Laying a chemical trail is a 'mass recruitment' system enabling a single individual to recruit a large number of other individuals with its pheromone trail.

Self-organization in bees that do not lay a scent trail comes about very differently. Honeybee colonies adjust the rates of recruitment and abandonment for each food

source in relation to its profitability. As a consequence they exploit more profitable food sources more intensively (Seeley et al. 1991). The number of foragers at different food sources is a result of (1) recruitment (positive feedback) and (2) abandonment (negative feedback). Each forager knows only about its own particular food source and evaluates the energetic gains and costs to estimate food profitability. If its estimate is high, recruitment will follow; if profitability is gauged as low, the individual forager will abandon the food source. 'Fine tuning' can be achieved by individuals adjusting the strength of their waggle dances, round dances and sound production to increasing and decreasing food qualities (Butler 1945; Boch 1956; von Frisch 1965; Waddington 1982; Seeley & Towne 1992; Waddington & Kirchner 1992; Seeley 1994, 1995; Seeley et al. 2000; de Marco & Farina 2001; Fernández & Farina 2002). This modulation of the individual's behaviour obviously suffices to account for the ability of the entire colony to select among food sources. (3) In honeybee colonies, multiple interactions occur between signallers and other individuals. One honeybee can recruit only a certain number of nestmates because only a limited number of nestmates can follow a dancing bee. In such a system the number of recruits is mostly determined by the number of signallers rather than by the number of potential recruits available as in scent trail-laying species (Dornhaus et al. 2006).

The decision making during foraging in stingless bees that do not lay a scent trail resembles that of honeybees rather than that of scent trail-laying stingless bees. *Melipona* colonies have been shown to forage as a self-organized superorganism in which individuals make decisions based on simple rules, which correspond at least partly with those of honeybees (Biesmeijer et al. 1998; Biesmeijer & Ermers 1999). *Melipona* bees adjust their vibrational and sound signals inside the nest to food profitability (Aguilar & Briceño 2002; Nieh et al. 2003; Hrncir et al. 2004). Hence, a specific adjustment of positive feedback (recruitment, reactivation) and negative feedback (abandonment) leads to an increased allocation of the foraging force to the most profitable food source (Biesmeijer & Ermers 1999).

Effectiveness of Scent Trail Laying

We found an underexploitation of the richer food source by *T. recursa* when it was discovered later than the poorer one. We conclude that communicating the location of the food source by scent trails limits a colony's ability to switch to newly discovered food sources. This does not necessarily reduce the effectiveness of collective foraging. Scent trail laying is mostly used by species with large colony sizes (stingless bees: Lindauer & Kerr 1958; Jarau et al. 2003; ants: Beckers et al. 1989; Jaffe & Deneubourg 1992). For these, flexibility in the allocation of the foraging force is not crucial because the pool of unemployed nestmates is not easily exhausted. There will still be recruits to exploit a richer food source discovered later even with a large number of recruits already collecting at the poorer food source. This is known in ants (Bonabeau

et al. 1998) and we have now demonstrated this for stingless bees as well. Hubbel & Johnson (1978) postulated that in scent trail-laying stingless bees the slow recruitment to new food sources is compensated by the ability to monopolize food sources against other species. The astounding accuracy with which stingless bees laying a scent trail find a food source supports the idea that there was no major selection pressure on the ability to switch promptly to a better food source (Lindauer & Kerr 1958; Hubbel & Johnson 1978; Schmidt et al. 2003; Sánchez et al. 2004). Because hardly any colony member gets lost on the way to the food source the probability of encountering new (maybe more valuable) food sources is reduced. Obviously, the colony's benefit from intensively exploiting a sufficiently profitable food source until its depletion outweighs the virtual costs of neglecting more valuable food sources and the real costs of reallocating busy foragers to a newly discovered feeding site.

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