



Experience-based interpretation of visual and chemical information at food sources in the stingless bee *Scaptotrigona mexicana*

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Eusocial bee (Apidae) foragers are able to mark food sources with olfactory attractant or repellent signals. Because these bees also have an excellent ability to learn associatively, they may be able to associate forager-deposited marks either positively or negatively with food depending on reward quality. We provide the first field experiments showing such a context-based interpretation of field information (odour marks and visual local enhancement) in stingless bees. We sequentially exposed individual foragers of the stingless bee *Scaptotrigona mexicana* to three situations in which one feeder was marked with either the visual presence of nestmates (sealed inside clear containers to prevent odour release) or odour marks alone. In the first situation, we offered two equally rewarding sucrose feeders (unscented 2.5 M sucrose solution). In this case, experienced foragers showed no preference on their subsequent visits to any of the feeders, even though the marked feeder was made more conspicuous with odour marks or the visual presence of nestmates. In the second situation, experienced foragers significantly preferred the marked feeder when it offered a sucrose reward. In the third situation, when the marked feeder offered no carbohydrate reward (only water) and the unmarked feeder offered sucrose, the experienced foragers avoided the marked feeder and significantly preferred the unmarked one. Thus, foragers learned to associate food quality positively or negatively with chemical or visual marks at the food source.

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Foragers of highly social bees (Hymenoptera, Apidae) collect food for the survival of an entire colony. This requires substantial effort and thus some species have evolved the ability to recruit nestmates (von Frisch 1967). In particular, the stingless bees (Apidae, Meliponini) recruit nestmates through communication mechanisms

classified as either field based (performed outside the colony) or nest based (performed inside the colony). Field-based communication mechanisms improve location communication through olfactory and visual (social facilitation) signals when several food alternatives are present (Villa & Weiss 1990; Slaa et al. 2003; Jarau et al. 2004; Sánchez et al. 2004, 2007; Schmidt et al. 2005).

Olfactory signals can substantially increase the foraging efficiency of social bees (Giurfa 1993; Goulson et al. 1998, 2001). In the honeybee, *Apis mellifera*, food-only odour marking plays a role in forager orientation and can indicate food profitability in the field (von Frisch 1967; Giurfa 1993). Similarly, studies have shown that bumblebees (*Bombus* spp.) evidently use different compounds to

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odour-mark food sources, with either attractants or repellents (Goulson et al. 2001). Stingless bees use diverse strategies to deposit odour marks (Jarau et al. 2002, 2004; Hrnčir et al. 2004; Nieh 2004). For example, they can leave complete odour or partial odour trails or odour-mark the food source alone. However, thus far, no study has conclusively demonstrated the existence of repellent odour marking in any stingless bee species.

The presence of nestmates at the food source can modify substantially the behaviour of arriving foragers, a phenomenon called social facilitation (Slaa et al. 2003). Some field results support the idea that forager experience at source influences forager interpretation of the mark as an attractant or as a repellent (Biesmeijer & Slaa 2004). For example, Slaa et al. (2003) found that foragers of the stingless bee *Trigona amalthaea* prefer a feeder with nestmates on it during their first arrival (local enhancement). However, in subsequent visits, they switch their preference to an unoccupied feeder (local inhibition). Thus, experience with the food source and nestmates on the food may lead foragers to change their orientation preferences.

Foragers can also interpret odour marks as attractive or repellent, depending on the quality of the food, the experience of the information recipient, or both (as in bumblebees, Saleh & Chittka 2006; Witjes & Eltz 2007). At natural food sources, marks may switch from attractive to repellent because of rapid food depletion or a slow rate of nectar replenishment. These changes would lead to a negative association between the odour marks and the resource. In the opposite situation, foragers could be exposed to odour-marked profitable food sources and thus form a positive association between these odour marks and the food. Foragers may therefore form positive or negative associations with odour marks, depending on their most recent experience. This experience that foragers gain with changes in food-source profitability may be an important factor affecting their choice behaviour within and between patches (Menzel 1999).

Thus, we propose that stingless bees (like their close relatives, bumblebees, Cameron & Mardulyn 2001) share an ability to form negative or positive associations with forager-borne marks (either olfactory or visual). In this way, experience would allow foragers to interpret field-based information according to the context, allowing recruits to reject or to accept visually or odour-enhanced flowers. We therefore investigated the possible interpretation of social facilitation and odour marks as either attractive or aversive signals in the stingless bee *Scaptotrigona mexicana* (Apidae, Meliponini). This species inhabits southeastern Mexico, where it shares resources with at least 30 other species of stingless bees (Ayala 1999). Feral colonies of *S. mexicana* range from 2000 to 5000 individuals, display efficient recruitment communication (Sánchez et al. 2004) and use odour marks deposited on the food source. Foragers also use social facilitation and show high-precision within-patch recruitment (Sánchez et al. 2007), as observed in other stingless bee species (Schmidt et al. 2003). Our goal was to determine whether chemical or visual marks could operate as repellents or as attractants. We therefore tested whether (1) odours

deposited by nestmates or (2) the presence of nestmates would trigger attraction or avoidance depending upon a forager's previous experience with food profitability.

METHODS

Study Site

We conducted the experiments on the campus of El Colegio de la Frontera Sur, in the city of Tapachula, Chiapas, Mexico (14°53'N, 92°17'W) from April to May 2004 and from April to May 2006 (from 0900 to 1400 hours). We successively used three colonies of *S. mexicana* housed in wooden boxes (50 × 25 × 20 cm) kept inside the laboratory, with a 3 cm diameter tube through the wall to allow outdoor foraging. After completing experiments with each colony, we moved it to a field site located 10 km away from the experimental field to prevent formerly trained foragers from returning to the feeder arrays. The populations in the colonies were determined visually to be approximately 2500–3000 bees each, thus representing normal-sized *S. mexicana* colonies with healthy amounts of brood and food reserves.

Bee Training

To evaluate the context-based interpretation of chemical and visual marks, we first trained five foragers to collect food from a feeder located 4 m south of the nest. The feeder consisted of a 0.5 cm diameter cotton ball soaked in 0.5 ml of unscented, analytical-grade 2.5 M sucrose solution placed on a plastic petri dish (5.5 cm diameter), with a yellow card inside. We define a clean feeder as one that foragers have never visited and thus does not contain any potential forager-deposited odour marks. We placed the feeder on the top of a 1.0 m high plastic stool. The foragers were individually marked on their thorax with colour painting. We tested only one forager at any given time and trapped the others within corked glass tubes 10 × 1 cm in size. We tested the focal forager according to the type of experiment being conducted (see below). We captured all unmarked recruits arriving at the set-up during the training phase with corked glass tubes and then transferred them to sealed plastic bags. We subsequently marked all captured bees with colour painting on their thorax. We then released these marked bees at the end of each day to avoid depleting the colony of foragers. We used each of the focal foragers only once to avoid pseudoreplication. On subsequent days, we captured any marked foragers visiting the feeders before the beginning of the trials.

Experiments

We conducted four control experiments and one main experiment, as outlined below. We present the detailed methodology under **Results** to aid the reader. First, we performed four control experiments to test the interpretation of chemical and visual marks with sucrose solution

(rewarding) versus water (unrewarding). We therefore examined whether *S. mexicana* foragers (1) discriminate water from sucrose by smell, (2) odour-mark attractively or repellently and (3) use social facilitation. Then we performed the main experiment to determine whether the foragers could learn to associate odour marks or visual forager presence with changes in profitability over time.

Statistics

We analysed the data from the control experiments with chi-square statistics, according to the design of each experiment and with a null hypothesis expectation of a uniform distribution. The data from the context-based experiment are repeated measures. Thus, to include the repeated measurement component of these data, they were analysed with ANOVA for repeated measures, to detect significant differences across visits (Giurfa 2004), and generalized additive models (Hastie 1993), to discover potential in our binomial data.

RESULTS

Control Experiments

Experiment 1: can S. mexicana foragers differentiate between sucrose and water?

Reagent-grade sucrose solution is odourless to honeybees (Tautz & Sandeman 2003), but it is not known whether this is also true for stingless bees. Thus, we first determined whether foragers of *S. mexicana* could differentiate between distilled water and reagent-grade sucrose solution. To determine whether the odour of sucrose solution could attract newly arriving recruits, we trained one *S. mexicana* forager on a single feeder as described above. After 20 min, we removed the training feeder (sealing it inside a plastic bag to prevent odour release) and set out two clean identical feeders at the feeding site (separated from each other by 30 cm). One feeder offered water and the other a 2.5 M unscented reagent-grade sucrose solution. We captured and sealed each recruit in a glass tube and recorded its choice in the absence of any other bee to eliminate the possibility of visual local enhancement. In 10 repetitions, 109 newcomers visited the sucrose feeder, whereas 98 visited the water feeder, a nonsignificant difference ($\chi^2_1 = 2.64$, $P = 0.104$).

To investigate the effect of the odour of sucrose solution in experienced foragers, we presented one trained *S. mexicana* forager with two feeders, one with 2.5 M sucrose solution and the other with distilled water, both in pieces of cotton. After the test bee landed, we exchanged the chosen feeder with a clean one to avoid any orientation by odour marks. We recorded 20 consecutive choices per experienced forager. Any recruit arriving at this set-up was immediately trapped with a suction tube to avoid marking by this bee. In 10 repetitions ($N = 10$ foragers, $n = 200$ choices, 20 consecutive choices per forager), experienced foragers visited the sucrose feeder 111 times and the water feeder 89 times (no significant difference, $\chi^2_1 = 2.42$, $P = 0.120$). Thus, we used distilled water and

sucrose in our subsequent experiments because *S. mexicana* foragers evidently cannot discriminate between unscented sucrose solution and pure water based upon odour.

Experiment 2: how many forager visits are necessary to deposit attractive odour marks?

Hrncir et al. (2004) found that a minimum of 40 visits is necessary for *Melipona seminigra* foragers to odour-mark a feeder attractively. To determine the minimum number of visits necessary for *S. mexicana* foragers to deposit attractive odour marks, we trained five foragers to odour-mark three feeders at different levels by controlling the number of times that the foragers landed on each feeder (10, 30 or 50 landings, respectively). After obtaining these three levels of odour marking, we sealed the three feeders in separate plastic bags. We then set out a clean feeder and let the trained foragers visit it and recruit at it freely. During 10–20 min, any newly arriving recruit was gently trapped with a glass tube and marked with a different combination of paint colours on its thorax to distinguish it from the trained foragers. After we trapped 8–10 recruits, the trained foragers were caught. Next, we removed the visited feeder and released the trapped recruits. When no bee was seen flying over the set-up (indicating that the recruits were no longer searching in the set-up vicinity), we set out the three odour-marked feeders and injected 5 ml of sucrose into the colony to reactivate foraging. We then recorded the choices made by reactivated recruits in the absence of the trained foragers. We found, in eight repetitions, a significant difference between choices for the feeders. The reactivated foragers landed preferentially on the feeder that had been visited 50 times over the two other feeders (10 times, 21 foragers; 30 times, 21 foragers; 50 times, 42 foragers; $\chi^2_2 = 10.5$, $P < 0.05$). Thus, *S. mexicana* foragers can odour-mark a good food source attractively, and the feeder that was visited 50 times was the most attractive. Based upon these results, we used feeders that had been visited 50 times for our odour-marking experiments.

Experiment 3: can foragers deposit repellent odour marks?

In addition to depositing attractive odour marks, *S. mexicana* foragers may deposit repellent odour marks. In experiment 3A, we tested for repellent marking by simultaneously offering 2.5 M sucrose solution and water in two separate feeders (spaced 30 cm apart and 4 m south of the colony) to five marked foragers for 10 min. This simulates a partially depleted patch. We captured all arriving recruits with a suction tube before they fed. During this procedure, the trained foragers consistently visited the water feeder, landing on it multiple times, and thus had the opportunity to deposit repellent odour marks. Next, we removed and sealed the five trained bees inside glass tubes. We then released the trapped newcomers and allowed them to choose between a new, clean feeder and the feeder putatively marked with repellent, both offering sucrose solution. To eliminate potential visual local enhancement (Slaa et al. 2003), we counted only

individual choices made in the absence of any other bees on the feeders. In two repetitions, newcomers showed no significant aversion to any feeder putatively odour-marked with repellents compared to control feeders (control feeder: 34 bees; marked feeder: 29 bees; $\chi^2_1 = 0.396$, $P = 0.528$).

In experiment 3B, we placed a feeder offering 2.5 M sucrose 4 m south from the colony and trained a group of 20–25 marked foragers to this feeder for 10 min. Next, we replaced this sucrose feeder with a water feeder and offered it to the foragers for 10 min more. We then sealed the odour-marked sucrose feeder inside a plastic bag. This set-up simulated a food patch changing from profitable to unprofitable. After 10 min of recurrent landings, no forager was seen searching around this previously visited water feeder. We then injected 5 ml of sucrose solution into the subject colony's entrance, to renew the foragers' interest in the feeder, and set out the previously visited feeder and a clean control feeder as in experiment 3A (both offering sucrose). We scored forager choices as in experiment 3A, counting only the choices of unmarked foragers (newcomers). As in the previous experiment, in two repetitions, there was no evidence for repellent marking (control feeder: 22 bees; marked feeder: 33 bees; $\chi^2_1 = 2.2$, $P = 0.138$). Thus, *S. mexicana* foragers evidently do not odour-mark unprofitable food sources as repellent.

Experiment 4: how many bees are required to elicit visual social facilitation?

To determine the minimum number of bees necessary to elicit either visual local enhancement or visual local inhibition, we trained one forager to feed on a training feeder (T) placed on top of a sealed petri dish containing one, three or five visible bees. We sealed the petri dish (5.5 cm diameter) with Parafilm stretched around the dish to prevent any leakage of odours from these trapped bees. After 20 visits (always using new, clean, unvisited feeders to prevent foragers from depositing odour marks), we presented the forager with a new set-up. In addition to the training feeder, we set out two new feeders (F) on top of sealed petri dishes with bees. We tested the attraction to various numbers of sealed bees. For example, we presented a training feeder containing one bee (T1) and one new feeder containing three bees (F3). We used the following combinations: T1 versus F3 and F5; T3 versus F1 and F5; T5 versus F1 and F3. In six repetitions (two repetitions for each set-up, $N = 60$ bees, one choice per bee), foragers showed no significant preferences in any of the three set-ups (T1 versus F3 and F5: foragers at each feeder, 8, 6, 6, respectively: $\chi^2_2 = 0.400$, $P = 0.819$; T3 versus F1 and F5: foragers at each feeder, 6, 6, 8, respectively: $\chi^2_2 = 0.700$, $P = 0.705$; T5 versus F1 and F3: foragers at each feeder, 5, 8, 7, respectively: $\chi^2_2 = 0.700$, $P = 0.705$). In addition, we found no significant difference in the distributions of the foragers between the set-ups ($\chi^2_4 = 0.00$, $P = 0.831$). Thus, we chose the feeder showing one bee for further experiments to reduce handling time and colony disturbance.

We also tested an empty feeder against a feeder with one bee inside. In the statistical analysis of this experiment, we considered newcomers and reactivated foragers separately.

Both types of foragers significantly preferred the occupied feeder (newcomers on empty feeder: 10; newcomers on occupied feeder: 35; $\chi^2_1 = 13.889$, $P < 0.001$; reactivated bees on empty feeder: 19; reactivated bees on occupied feeder: 49; $\chi^2_1 = 13.235$, $P < 0.001$). Therefore, *S. mexicana* foragers can use visual local enhancement, and the visual stimuli provided by a single nestmate on the food is sufficient to elicit attraction.

Main Experiment

Experiment 5: can foragers learn to associate odour marks or visual forager presence with changes in profitability over time?

To determine whether foragers can learn to associate odour marks or nestmate presence with profitable or unprofitable food, we conducted an experiment consisting of 30 choices divided into three situations. For the odour-marking experiments (OME), before beginning each repetition, we allowed the marked forager to visit the training feeder 50 times, potentially to odour-mark it. For the social facilitation experiments (SFE; testing nestmate presence), we trained one forager to feed on a sealed petri dish (2.5 M sucrose solution) containing a nestmate (see experiment 4 procedure). Just before starting the experiment, we set out a clean feeder with a nestmate inside to prevent foragers from using any potential odour mark left during training. Hereafter, we refer to both the odour-marked feeder and the feeder visually enhanced with a nestmate as the 'marked' feeder.

Situation 1

We randomly moved the marked feeder to the left or to the right of the feeder stand and placed a new, unmarked, identical feeder 30 cm away on the opposite side. Both feeders offered the same reward (2.5 M sucrose). In this way, we evaluated the fidelity of the forager to the marked feeder in the presence of an equally profitable food source. We allowed only 10 visits to this set-up (each visit equaling one choice). To keep the focal forager from local landmark learning, we rotated the feeder array pseudorandomly (predetermined anti- and clockwise rotations such that all feeders were placed in all positions). Additionally, in the OME, if the forager visited the control feeder, we immediately replaced this feeder with a new, clean, unvisited one to remove potential scent marks. We repeated this procedure in situations 2 and 3. In the SFE, each time the focal forager landed on any feeder, we swapped out this feeder with a corresponding new feeder (marked or unmarked). We did this in situations 2 and 3 as well. We recorded 10 choices of the focal forager. Not surprisingly, foragers showed no significant preference for either feeder across the 10 visits (ANOVA for repeated measures: OME: $F_{9,171} = 2.239$, $P = 0.022$; SFE: $F_{9,171} = 0.991$, $P = 0.446$).

Situation 2

In this experiment, we tested whether the focal forager was able to associate the mark (visual or olfactory) with an

unprofitable food source. Immediately after the 10th visit of situation 1, the same forager was confronted with a new challenge: it had to choose between the marked feeder (now offering water) and the unmarked feeder still offering the same sucrose solution. We then allowed and recorded another 10 choices. In this situation, foragers significantly preferred the unmarked feeder in the OME, but not in the SFE (ANOVA for repeated measures: OME: $F_{9,171} = 2.862$, $P = 0.004$; SFE: $F_{9,171} = 1.717$, $P = 0.078$). Thus in this situation, odour marks, not forager visual presence, evidently enhanced forager ability to pick the rewarding feeder correctly.

Situation 3

After 10 choices performed in situation 2, we reversed the conditions and thus restored the original condition (the marked feeder now offered sucrose and the unmarked offered water). We allowed and recorded another 10 choices. Under this new condition, foragers were attracted to the marked training feeder over the unmarked control feeder in both OME and SFE (ANOVA for repeated measures: OME: $F_{9,171} = 3.614$, $P < 0.001$; SFE: $F_{9,171} = 12.638$, $P < 0.001$).

Overall, we used 40 bees and recorded 1200 forager choices: half for the SFE and half for the OME (Fig. 1). Table 1 summarizes the choice frequencies observed in this experiment. We fitted the data of this experiment with a generalized additive model (Fig. 2). The curve observed in the OME (generalized additive model: $\chi^2 = 99.62$, $P < 0.001$) and the SFE (generalized additive model: $\chi^2 = 110.717$, $P < 0.001$) deviated from a random foraging pattern. There was no significant difference between the choice curve observed in the OME compared with the choice curve observed in the SFE ($F_{1,58} = 0.034$, $P = 0.854$). Thus, foragers can use odour marks or nest-mate presence to orient themselves towards food that is more profitable or to avoid unprofitable food.

DISCUSSION

Adapting to a changing environment is crucial for survival, and thus honeybees, bumblebees and, possibly,

stingless bees lay odour marks on food sources, according to food profitability (Goulson et al. 2001). However, the possibility of a context-dependent interpretation of odour marks and visual marks (forager presence) has received relatively little attention, although the effects of context, experience and learning on insect choice behaviour are well known (Biesmeijer et al. 1998; Biesmeijer & Ermers 1999). It is therefore possible that a visual or olfactory mark that can indicate rich food sources can also be interpreted to indicate poor food sources when the originally rich food source becomes exhausted or decreases in quality. We found this to be the case with the stingless bee *S. mexicana*.

Changing Environment and Fidelity

Bee foragers often show fidelity to a location or to a certain floral morphotype, provided it remains a continuously profitable food source. Fidelity is established through the learning of the key characteristics of the resource (Collett 1992; Slaa 1998; Wilson 2000). We therefore expected the foragers to associate the mark (either odours or nestmates) with a profitable food source very rapidly and thus to prefer the training feeder with the mark to a control feeder without the tested mark. This hypothesis is supported by evidence from studies on *Apis mellifera* wherein the acquisition of information was based on an absolute conditioning procedure, as in this work (Chittka et al. 2003; Giurfa 2004). However, with *S. mexicana*, this was not the case, and the foragers seemed not to use the orientation information given to indicate the training feeder, perhaps because the two feeders were placed very close to each other. In situation 1, the foragers chose randomly between the two feeders. They did not show any fidelity to the training (marked) feeder. The low degree of fidelity observed here has also been observed in experiments with other species of stingless bees and in honeybees (Gould & Gould 1988; Slaa 1998; Slaa et al. 2003). However, the differential marks in those experiments were neither odour marks nor resident nestmates but food source attributes such as colour or shape.

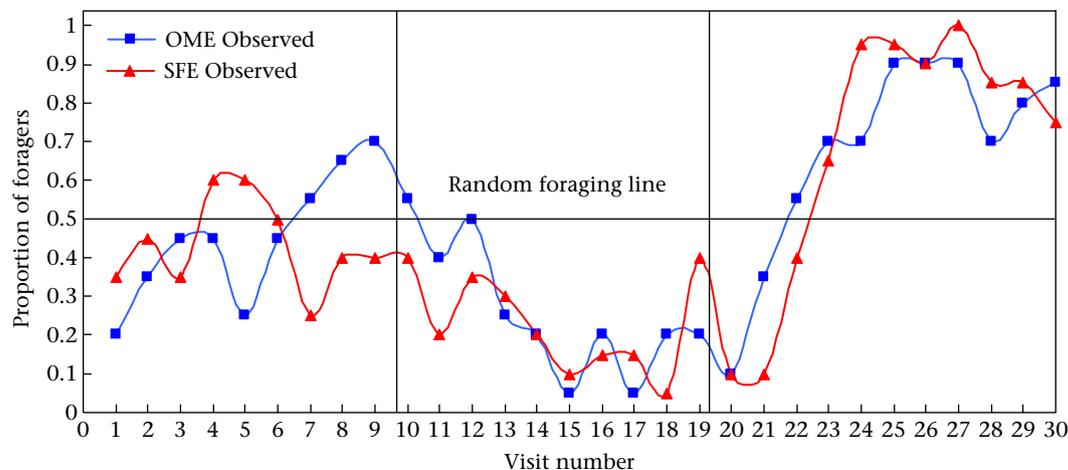


Figure 1. Choices over time in the odour-marking (OME) and the social facilitation (SFE) experiments. The proportion of bees choosing the training feeder is shown. The two vertical lines at times 10 and 20 represent the end of situations 1 and 2, respectively.

Table 1. Descriptive statistics for the choice frequencies on the training feeder

	Odour marking				Social facilitation			
	Lowest	Highest	Average	Standard deviation	Lowest	Highest	Average	Standard deviation
Situation 1	2	9	4.6	1.7	1	6	4.3	1.5
Situation 2	0	6	2.2	1.7	0	5	2.0	1.4
Situation 3	5	9	7.3	1.3	6	9	7.4	0.9

Highest and lowest: the minimum and maximum number of choices made by foragers in every situation.

In our set-up, both food sources were equally profitable and thus a preference for one over the other was not rewarded. This result, and the fact that the feeders were almost identical (except for the differential mark), suggests that the foragers had no advantage in preferentially choosing the marked feeder. Wells et al. (1992) obtained a similar result in a different set-up: honeybee foragers did not discriminate between blue and yellow shapes if they offered the same reward. However, it might also be possible that the foragers actually learned that any feeder-like structure on the foraging site was profitable, that is, they learned to visit any feeder regardless of odour marks or visual enhancement.

In the next 20 visits, when the feeders offered different resources (water in one feeder, sugar in the other), the bees initially failed to choose the richest feeder. However, after a few trials, they began to show fidelity to the unmarked feeder (situation 2) or to the marked feeder (situation 3), as shown in Figs 1 and 2. This may be interpreted in an ecological context as foragers adapting from a stable situation to a changing one through experience and learning. Through learning, foragers can thus modify their behaviour to handle new situations to keep bringing food to the colony.

Foragers could have deposited repellent odour marks in the marked feeder in situation 2, but marked it attractively in situation 3. The feeders in situations 2 and 3 could therefore present a mixture of repellents and attractants.

However, this is unlikely because we found no evidence of repellent marking in the *S. mexicana* repertoire of communication mechanisms (experiment 3). Thus, unless food profitability changes, foragers will keep collecting the same resource in the same place (i.e. a high flower constancy). Otherwise, foragers will switch to different food sources, in space or time, learning the features of the new resource and adjusting their efforts to new locations (Gould & Gould 1988; Biesmeijer & Ermers 1999; Menzel 1999). Potential sources of odour marks in this species can be found in the labial glands. In preliminary experiments with *S. mexicana* (unpublished data), we found that foragers prefer feeders baited with a labial gland extract rather than with pure hexane. Similar results have been reported by Jarau et al. (2004) for *Trigona recursa* and by Schorkopf et al. (2007) for *Trigona spinipes*. Compounds that have been shown to elicit scent trail following-like behaviour in these species are hexyldecanoate in *T. recursa* (Jarau et al. 2006) and octyloctanoate in *T. spinipes* (Schorkopf et al. 2007). Surprisingly, despite these species being closely related, these compounds are rather different. Hence, further bioassays to identify the potential compounds responsible for food marking in *S. mexicana* should be conducted.

Similar patterns of foraging adaptation have been observed in *A. mellifera* (Giurfa 2004) and *Bombus terrestris* (Dyer & Chittka 2004), but using feeder colours as the source of differential information instead of forager-

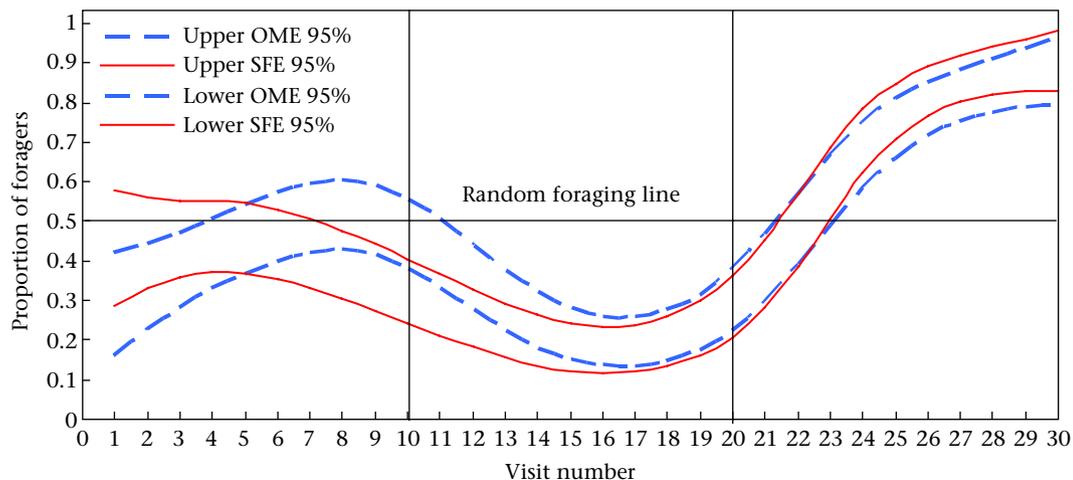


Figure 2. Generalized additive model for the proportion of the foragers that chose the training feeder in the three situations. Upper and lower limits for the odour-marking (OME) and the social facilitation (SFE) experiments are shown.

associated marks. In our set-up, the bees had to rely on another source of information to choose correctly. Because the feeders were identical in shape, colour and size, the only marks that foragers could use were forager-deposited odour marks or the presence of a nestmate. The foragers adapted to the changes and learned to associate these marks with the lower-quality food source.

Context-based Interpretation

Our results show that *S. mexicana* foragers use odour marks in an experience- (i.e. context)-based way. The marks worked as repellents when the profitability associated was low (training feeder with water) and as attractants in the opposite situation (training feeder with sucrose). For this to occur, foragers had to learn through experience. Slaa et al. (2003) reported that the more visits a *T. amalthaea* forager makes to a food source, the more likely that forager will switch from local enhancement (the presence of a nestmate as an attractive mark) to local inhibition (nestmate as a repellent mark). However, it is not clear whether it was the presence of nestmates or other factors that elicited this behavioural change. Similar data were obtained by Saleh & Chittka (2006) and Witjes & Eltz (2007) with *B. terrestris*, but using odour marks as the differential mark. The authors therefore hypothesized that a single mark may operate as a stimulus with two inputs, which are defined by experience and context.

In our study with *S. mexicana*, we show that the presence of a nestmate or odour marks can be positively or negatively associated with a food source. Moreover, both odour marks and nestmate presence evidently gave similarly reliable information. The foragers interpreted these sources of information according to context and experience. The use of information was therefore not functionally fixed, but context based.

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