ANIMAL BEHAVIOUR, 2008, 76, 407–414
doi:10.1016/j.anbehav.2008.04.003

Available online at www.sciencedirect.com
ScienceDirect

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

DANIEL SÁNCHEZ*, JAMES C. NIEH† & RÉMY VANDAME*‡
*El Colegio de la Frontera Sur, Chiapas, Mexico
†Division of Biological Sciences, Section of Ecology, Behavior, and Evolution, University of California, San Diego, U.S.A.
‡INRA–UMR Innovation, Montpellier, France

(Received 23 July 2007; initial acceptance 7 November 2007; final acceptance 30 January 2008; published online 4 June 2008; MS. number: A10823)

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.

Keywords: odour mark; *Scaptotrigona mexicana*; social facilitation; stingless bee; visual local enhancement

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

Correspondence: R. Vandame, El Colegio de la Frontera Sur, Carretera Antiguo Aeropuerto Km. 2.5, 30700 Tapachula, Chiapas, Mexico (email: rvandame@ecosur.mx, vandame@supagro.inra.fr). J. C. Nieh is at the Division of Biological Sciences, Section of Ecology, Behavior, and Evolution, University of California, San Diego, La Jolla, CA 92115-0116, U.S.A.

0003–3472/08/$34.00/0

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; Hrncir 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 amalthea* 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 ($50 \times 25 \times 20$ 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