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Original article

The use of food source scent marks by the stingless bee *Trigona corvina* (Hymenoptera: Apidae): the importance of the depositor's identity[1]

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Abstract – The deposition and use of scent marks on food sources has been found in foraging solitary bees, bumblebees, stingless bees and honeybees. The widespread existence of this communication mechanism points to its ecological significance. The importance of the depositor's identity on the use of food source scent marks, however, has never been systematically investigated in the same bee species. Here we present strong evidence that individual foragers of the stingless bee species *Trigona corvina* scent marked a high quality food source and that they used their own scent marks to relocate it in choice experiments. *T. corvina* foragers showed a similar significant preference for a food source scent marked by their nest mates and by bees from a conspecific colony over a non-scent marked food source. However, no evidence for the use of scent marks deposited by other stingless bee species was found. The implications of these findings for the evolution of food source scent marking in bees are discussed.

scent mark / food source / depositor / stingless bee / *Trigona* / chemical communication

1. INTRODUCTION

Social bees living in colonies, such as honeybees, bumblebees and stingless bees, need to exploit multiple food sources (e.g. flowers for pollen and nectar) efficiently to meet the high energy demands of their larvae and maintenance of the colony. In their joint efforts to achieve this, foragers are confronted with ephemeral and scattered food sources that are visited by other insects as well. A wide variety of food source communication mechanisms has evolved to face these temporal, spatial and ecological challenges (Nieh, 2004). One of the ways social bees communicate a flower's location and profitability in the field, is by depositing scent marks on it (Michener, 1974). The use of these chemical signals improves foraging efficiency: repellent scent marks reduce the time that is wasted in probing depleted flowers (e.g. Giurfa, 1993; Williams, 1998; Gilbert et al., 2001; Stout and Goulson, 2002), while attractant scent marks advertise the presence of rich food sources (e.g. von Frisch, 1967; Ferguson and Free, 1979; Free and Williams, 1983; Schmitt and Bertsch, 1990).

A single flower patch is often exploited by several bees and bee species simultaneously. Thus, apart from their own scent marks, individual foragers may encounter those deposited on flowers by nest mates, non-nest mate conspecifics and bees from other species as well. These circumstances may have led to the evolution of the ability to use all scent marks

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independent of the depositor's identity. Bumblebees (*Bombus* spp.) have already been found to detect and reject, with a high degree of accuracy, flowers that have been visited previously by themselves, conspecifics and other species of bumblebees (Goulson et al., 1998, 2000; Williams, 1998). Honeybee workers (*Apis mellifera*) deposit scent marks that attract recruited nest mates to previously visited profitable food sources (von Frisch, 1967; Ferguson and Free, 1979; Free and Williams, 1983). In addition, the own and nest mate scent marks were shown to be used to avoid visiting flowers recently depleted of nectar (Giurfa, 1993; Williams, 1998). However, whether honeybees and bumblebees can use each other's food source scent marks remains to be clarified, for contradictory results have been published; honeybees and bumblebees showed no reaction to each other's scent marks in a field study by Williams (1998), whereas a strong repellent effect of the other species' scent marks was described in later field studies (Stout and Goulson, 2001).

The common phenomenon of food source scent marking has been studied in a number of stingless bee species as well. The stingless bee species *Melipona favosa* (Aguilar and Sommeijer, 2001) and *Plebeia tica* (Aguilar et al., 2004a) have been found to use their own scent marks to relocate a high quality food source. Nearly all other research on scent marking in stingless bees addresses the use of scent marks deposited on the food source by nest mates. For example, *M. panamica* (Nieh, 1998), *Trigona fulviventris* (Goulson et al., 2001), *M. mandacaia* (Nieh et al., 2003a), *T. hyalinata* (Nieh et al., 2003b), *Scaptotrigona depilis* (Schmidt et al., 2003), *Plebeia tica* (Aguilar et al., 2004a), *M. seminigra* (Hrncir et al., 2004), *T. recursa* (Jarau et al., 2004), *T. spinipes* (Nieh et al., 2004a), *M. rufiventris* (Nieh et al., 2004b) and *Nannotrigona testaceicornis* (Schmidt et al., 2005) are attracted to nest mate scent marks when given the choice between a clean food source and one scent marked by nest mates or baited with their glandular extracts.

The use of food source scent marks deposited by stingless bees from a conspecific colony seems to have been investigated only in *Tetragonisca angustula* (Villa and Weiss, 1990) and *Nannotrigona testaceicornis* (Schmidt et al., 2005). Foragers' responses to a feeder scent marked by bees from another conspecific colony were similar to those in which the scent marks came from their own colony; the foragers made significantly more visits to the scent marked feeder than to a clean control feeder (Villa and Weiss, 1990; Schmidt et al., 2005). *Tetragonisca angustula* was also studied regarding its use of heterospecific scent marks (Villa and Weiss, 1990). When *T. angustula* bees were offered the choice between a dish scent marked by nest mates and a dish scent marked by foragers of another stingless bee species (*T. peckolti*), all visits were made to the dish with the nest mate scent marks (Villa and Weiss, 1990). However, this finding does not necessarily indicate that stingless bees can not use other stingless bee species' scent marks, but merely that nest mate scent marks were preferred over heterospecific scent marks by *T. angustula* foragers.

Indeed, recently it has been shown that stingless bees do make use of heterospecific scent marks. Naive foragers of the stingless bee species *Trigona spinipes* strongly preferred scent marks deposited by *Melipona rufiventris* over nest mate scent marks on food sources at new locations (Nieh et al., 2004b). *M. rufiventris* foragers, on the other hand, avoided scent marks deposited by *T. spinipes* foragers. The interspecific use of scent marks (termed "olfactory eavesdropping" by Nieh et al., 2004b) may be advantageous for aggressive species to detect and take over valuable food sources discovered by other bees, as well as for less aggressive species to avoid costly conflicts at sites being exploited by superior competitors (Nieh et al., 2004b).

Whether the use of scent marks is individual-specific, colony-specific, species-specific or genus-specific has never been addressed systematically in a single (stingless) bee species. Study of these issues may improve our understanding of the function and phylogeny of this food source communication mechanism. We investigated the importance of the scent mark depositor's identity in *Trigona corvina* (Hymenoptera, Apidae, Meliponini), a mass-recruiting species from the same genus as several other stingless bee species that have been reported to scent mark food sources (e.g. *T. mexicana*, Villa and Weiss, 1990; *T. fulviventris*, Goulson et al., 2001; *T. hyalinata*, Nieh et al., 2003b; *T. recursa*, Jarau et al., 2004 and *T. spinipes*, Nieh et al., 2004a, b). *Trigona corvina* has been observed to repeatedly land on the food source during recruitment (Aguilar and den Held, 2003; Aguilar et al., 2004b, 2005), behaviour that may be indicative of scent marking (Jarau et al., 2004). *T. corvina* can be categorized as an "extirpator" species that aggressively displaces rivals from monopolized food sources (Johnson, 1983).

The aim of this study was to answer the following research questions: (1) Do *T. corvina* foragers scent mark a high quality food source and if so, do they use their own scent marks to relocate the food source? and (2) Do *T. corvina* foragers use scent marks deposited by nest mates, by conspecifics from another colony or by foragers from a different stingless bee species to relocate a food source?

2. MATERIALS AND METHODS

2.1. Study site and bee colonies

The experiments were carried out at the CINAT, Universidad Nacional, Heredia (10º 01' N, 84º 07' E), Costa Rica from December 2003 to April 2004. Two colonies of *Trigona corvina* Cockerell in their natural exposed nests (estimated worker populations of at least 4000 adult bees) and one colony of *Melipona beecheii* Bennett installed in a wooden observation box (estimated worker population of 500 adult bees), were used.

2.2. Feeders and training of bees

The training feeder consisted of a 65 cm high iron standard, to which a blue, circular cardboard plate (diameter 6.5 cm) was taped. The underside of the plate was scented with some drops of peppermint essence to facilitate training of the bees. A circular transparent plastic sheet (diameter 6.5 cm) with a feeding cup (the lid of an eppendorf-vessel) glued in the centre that was filled with 0.1 mL of 2.0 M unscented sugar water solution (henceforth called "feeding layer") covered the upside of the plate.

The two test feeders consisted of identical 65 cm high iron standards, to which yellow, rectangular cardboard plates (6.5 × 7.5 cm) were taped that were not artificially scented. The test feeder plates were covered with rectangular transparent plastic sheets on top of which circular transparent plastic feeding layers (diameter 6.5 cm) were attached. Thus, the training feeder differed in odour (peppermint-scented), shape (circular) and colour (blue) from the test feeders (scentless, rectangular and yellow, respectively). In this way we minimized any confounding effects of test subjects' artificial food source experience acquired during training, on their subsequent choices between scent marked and clean test feeders during the experiments (see Gould, 1993).

To train bees, the training feeder was placed in front of the nest entrance. As soon as a bee was observed to visit it repeatedly, we moved the feeder plus bee to the final training position at 15 m from the nest. A bee was considered trained upon its first return to and forage on the training feeder at the 15 m location.

For each experimental trial, we trained a single naive bee and marked it uniquely with a dot of paint on the thorax to facilitate recognition. Unmarked foragers subsequently arriving at the feeder (recruits) were captured with a suction tube, marked and released after the experiment. Training / test locations differed in direction between test subjects.

2.3. Experimental setup

In each of the four experiments conducted, individually trained and uniquely marked bees were offered the choice between two test feeders. One of these test feeders contained a feeding layer that was hypothesized to be scent marked previously by either (1) the test subject itself ("own scent mark experiment"), (2) the test subject's nest mates ("nest mate scent mark experiment"), (3) bees from a different colony of the same species ("conspecific scent mark experiment"), or (4) bees from a different species ("heterospecific scent mark experiment"). This feeder was thus called the M(arked)-feeder, whereas the other test feeder contained a clean feeding layer and was therefore called the U(nmarked)-feeder (Schmidt et al., 2003). Scent marks were collected on a clean feeding layer attached to the training feeder. To prevent the clean feeding layer from smelling like the peppermint scent from the underside of the training feeder plate, two extra circular transparent plastic layers were put in between the plate and the feeding layer.

For each trained bee we recorded whether it visited the M- or the U-feeder upon its first confrontation with the choice between the two test feeders positioned on opposite sides 50 cm from the training site (Fig. 1). A *visit* was defined as the landing *and* drinking of the trained bee on the feeder. To avoid any influences of local enhancement or inhibition (Slaa et al., 2003), only a visit of the trained bee to one of the test feeders while no other bees were at the feeders was defined as an individual choice and included in the analysis. All bees except the trained bee were captured upon arrival at the test feeders before they could land, to avoid any effect of scent marking by these bees. Side bias was counteracted

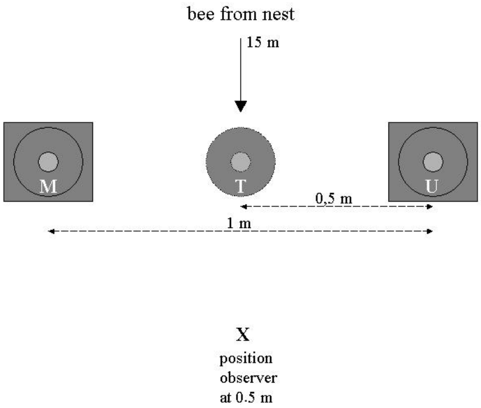

Figure 1. Feeder set-up. After training a bee to a location 15 m from the nest, the training feeder (T) was removed (indicated by the dotted contours). The trained bee was subsequently confronted with the choice between two test feeders (M and U) placed on opposite sides 50 cm from the training site. The M-feeder contained scent marks of the test subject itself, its nest mates, conspecifics or heterospecifics, respectively, whereas the U-feeder was a clean, unmarked feeder.

by randomly switching the positions of the test feeders between trials. Before handling the feeders and feeding layers, the experimenter always rinsed her hands with a 95% ethanol solution.

Neither local wind direction measured with a small flag at the training site, nor average wind strengths and directions obtained from the National Meteorological Institute, Aranjuez station, Costa Rica (09° 56’ N, 84° 05’ O), were found to affect the results (data not shown).

2.4. Own scent mark experiment

Once a bee was trained and given a unique paint mark, the feeding layer of the training feeder on which the bee had foraged was replaced by a clean feeding layer. After the trained bee had visited the clean feeding layer with unscented sugar water solution four times, this hypothetically scent marked feeding layer from the training feeder was removed to one of the two test feeders, making it the M-feeder, whereas the U-feeder contained a clean feeding layer. The M- and U-feeders were replenished with unscented sugar water solution and positioned on opposite sides of the training site. Upon its next return to the training site, the trained bee was confronted with the choice between the M-feeder, which presumably contained its own scent marks deposited during the bee’s previous four visits, and the clean U-feeder.

2.5. Nest mate scent mark experiment

A single bee was trained, uniquely marked and monitored to ascertain it consistently visited the training feeder. In the meanwhile, attempts to train another bee in a different direction from the training site of its nest mate were initiated. Once this second bee, the test subject, was trained and uniquely marked, the feeding layer on which its nest mate had been foraging for a minimum of 30 min [as it took at least 30 min to train a test subject] was transferred to the M-feeder. Immediately thereafter, the M- and U-feeders were replenished with unscented sugar water solution, positioned on opposite sides of the training site and the test subject was offered the choice between the M-feeder scent marked by its nest mate and the non-scent marked clean U-feeder.

2.6. Conspecific scent mark experiment

Procedures were identical to the nest mate scent mark experiment described above, with one exception: individual bees were offered the choice between an M-feeder of which the feeding layer had been visited for at least 30 min by only bees from another *T. corvina* colony, and a clean U-feeder.

2.7. Heterospecific scent mark experiment

Procedures were identical to the nest mate scent mark experiment described above, with one exception: individual bees were offered the choice between an M-feeder of which the feeding layer had been visited for at least 30 min by 3 to 6 bees from a *Melipona beecheii* colony [thus ensuring at least 40 *Melipona* visits (Hrncir et al., 2004)], and a clean U-feeder.

2.8. Statistical analyses

We pooled data of the first choices of all test subjects per experiment and used Chi-square goodness of fit tests to determine whether the distribution of bees over both feeders differed significantly from a random distribution. We rejected the null hypothesis when the *P*-value was smaller than the critical α-level of 0.05.

3. RESULTS

3.1. Do foragers scent mark a high quality food source and do they use their own scent marks?

Upon their first return to the training site, all trained bees tested ($n = 12$) visited the M-feeder

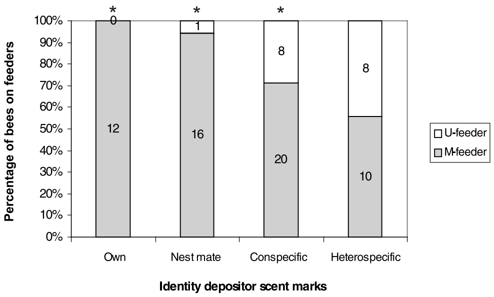

Figure 2. Percentages of bees landing on the M- and U-feeders for each of the four experiments conducted. The feeding layer of the M-feeder is scent marked by the trained bee itself, nest mates, conspecifics or heterospecifics, respectively. The U-feeder is a clean, unmarked feeder.
Numbers in bars represent sample sizes. *: $P < 0.05$. For statistics see text.

when presented with the choice between the clean U-feeder and the scent marked M-feeder. The distribution of bees over both feeders differed significantly from a random distribution (Chi-square test: number of bees visiting M-feeder vs. U-feeder: $n = 12$, $\chi^2_{0.05,\,1} = 12.00$, $P < 0.001$; Fig. 2, first column).

3.2. Do foragers use nest mate scent marks?

In their first choice between the M- and U-feeders, 94.12% of the bees tested ($n = 17$) visited the M-feeder scent marked by their nest mates. The distribution of bees over both feeders differed significantly from a random distribution (Chi-square test: number of bees visiting M-feeder vs. U-feeder: $n = 17$, $\chi^2_{0.05,\,1} = 13.24$, $P < 0.001$; Fig. 2, second column).

3.3. Do foragers use conspecific scent marks?

In their first choice between the M- and U-feeders, 71.43% of the bees tested ($n = 28$) visited the M-feeder scent marked by individuals from another *T. corvina* colony. The distribution of bees over both feeders differed significantly from a random distribution (Chi-square test: number of bees visiting M-feeder vs. U-feeder: $n = 28$, $\chi^2_{0.05,\,1} = 5.14$, $P = 0.023$; Fig. 2, third column).

3.4. Do foragers use heterospecific scent marks?

In their first choice between the M- and U-feeders, only 55.56% of the *T. corvina* bees tested ($n = 18$) visited the M-feeder hypothetically scent marked by *M. beecheii* foragers. The distribution of bees over both feeders did not differ significantly from a random distribution (Chi-square test: number of bees visiting M-feeder vs. U-feeder: $n = 18$, $\chi^2_{0.05,\,1} = 0.22$, $P = 0.637$; Fig. 2, fourth column).

4. DISCUSSION

The aim of this study was to determine whether the stingless bee species *Trigona corvina* deposits scent marks on a profitable food source and if so, whether experienced foragers use their own scent marks to relocate the food source. In addition, we investigated to what extent *T. corvina* foragers use scent marks deposited by nest mates, conspecifics from a different colony and stingless bees from a different species.

4.1. The use of the own scent marks

T. corvina bees were found to scent mark the food source and use their own scent marks to relocate the food source in choice experiments; a significant preference for the scent marked feeder was observed when trained bees were confronted with the choice between an unfamiliar feeder containing the own scent marks and a clean control feeder. Evidence for the use of the own scent marks to relocate the food source has now been found in the stingless bee species *Melipona beecheii* (F. Rojas, personal communication), *Melipona favosa* (Aguilar and Sommeijer, 2001), *Plebeia tica* (Aguilar et al., 2004a) and *Trigona corvina* (this study). The recruitment systems of these stingless bee species vary greatly in complexity and according to various phylogenies (Ascher et al., 2001; Costa et al., 2003; Michener, 2000), these species are not closely related. As the use of the own food source scent marks has also been observed in solitary bees (*Anthophora plumipes*; Gilbert et al., 2001), bumblebees (*Bombus* spp.; Goulson et al., 1998) and honeybees (*Apis mellifera*; Giurfa, 1993; Williams, 1998), this behaviour may have been present in a common ancestor of these four bee tribes.

The specific signalling function of the scent marks may be dependent on the profitability of the food source. In these and previous experiments on the use of the own scent marks by stingless bees (Aguilar and Sommeijer, 2001; Aguilar et al., 2004a; F. Rojas, personal communication), artificial food sources were used that offered a surplus quantity of nectar greatly exceeding the food storage capacity of the single test subject. Immediate revisits to the highly rewarding food source would increase foraging efficiency, which might be the reason trained foragers were always found to be attracted to their own food source scent marks. In field studies on honeybees (Williams, 1998) and bumblebees (Goulson et al., 1998) on the other hand, the own scent marks were observed to have a repellent effect on the depositor. In these experiments, natural flowers visited only 20 s (Williams, 1998) or 2 min (Goulson et al., 1998) previously were presented again to the same bee. In this short time span, floral nectar content could not have been replenished (Williams, 1998; Stout and Goulson, 2002). Therefore, the function of the repellent scent marks may be to prevent the depositors from wasting time and energy by revisiting empty flowers (Williams, 1998; Goulson et al., 1998). Both attractant and repellent effects of the own scent marks have been found in the solitary bee species *Anthophora plumipes* (Gilbert et al., 2001). Its scent marks seemed to be made up of short-term and long-term components. The long-term component (< 30 min) was initially repellent and matched the rate of nectar renewal, as was found for conspecific scent marks used by bumblebees (Stout and Goulson, 2002). The short-term component (< 3 min) of the scent marks deposited by the solitary *Anthophora plumipes* was observed to be attractive, resulting in a high level of immediate revisits that were advantageous in view of the amounts of nectar left behind upon the first visit (Gilbert et al., 2001).

Our findings suggest that *T. corvina* foragers used their own scent marks as a self-orientation signal to facilitate revisits to a high quality food source. It would be interesting to conduct field studies on this and other stingless bee species to investigate whether the own scent marks would be perceived as repellent when deposited on flowers that are depleted of nectar in one go, as found in the aforementioned studies on honeybees, bumblebees and solitary bees.

4.2. The use of nest mate scent marks

T. corvina foragers were shown to prefer visiting a food source scent marked by nest mates over a clean food source in our choice experiments. Attraction to nest mate scent marks in choice experiments has been found in numerous stingless bee species (see Introduction). It should be noted, however, that the test subjects in our experiments may have formed an association between their own scent marks and the profitable food source during the training phase. In the test phase, the bees may have been attracted to nest mates' scent marks because of their resemblance to the own scent marks, rather than reacting to the identity of the depositors per se.

Under natural circumstances, the function of stingless bee nest mate scent marks is thought to facilitate recruitment of naive bees to profitable food sources (Aguilar et al., 2004a; Nieh, 2004). Evidence for the use of attractant food source scent marks in recruitment has also been found in honeybees (von Frisch, 1967; Ferguson and Free, 1979; Free and Williams, 1983). If it is shown that bumblebees use attractant nest mate scent marks in recruitment (Dornhaus and Chittka, 2001) as do honeybees and stingless bees, this trait may have originated in the common ancestor of the eusocial bees (i.e. honeybees, bumblebees and stingless bees), after the group of solitary bees branched off in the phylogeny of bees.

4.3. The use of conspecific scent marks

T. corvina foragers were attracted by scent marks deposited on a high quality food source by bees from a conspecific colony. However, again we can not exclude the possibility that it was the similarity of the conspecifics' scent marks to the own scent marks, rather than the specific identity of the scent marks' depositors, that attracted the test subjects to the scent marked food source. To our knowledge, choice experiments on the use of food source scent marks deposited by conspecifics from another colony have been conducted with only the stingless bee species *Tetragonisca angustula*

(Villa and Weiss, 1990) and *Nannotrigona testaceicornis* (Schmidt et al., 2005). In both species, foragers preferred the artificial food source scent marked by bees from another conspecific colony over an unmarked one. In contrast, field studies on honeybees and bumblebees as well as on the stingless bee species *Trigona fulviventris* reported food source scent marks deposited by conspecifics to have a repellent effect (Goulson et al., 1998, 2000, 2001; Stout and Goulson, 2001; Williams, 1998), although it is unclear whether the conspecifics depositing the scent marks belonged to the test bees' own or another colony.

The use of repellent scent marks to avoid recently depleted flowers (as found in the field studies) and the use of attractant scent marks to exploit copious food sources (as found with the artificial food sources in choice experiments) by conspecific bees from another colony does not seem to confer direct fitness benefits to the depositors of these scent marks. Although the depositors' inclusive fitness would be increased by intraspecific scent mark use in case neighbouring colonies were founded by genetically related queens, *T. corvina* foragers from different colonies encountering each other on profitable food sources initiated fights to the death (Johnson and Hubbell, 1974). These observations suggest the use of conspecific scent marks in *T. corvina* to be a case of intraspecific "olfactory eavesdropping" (Nieh et al., 2004b).

4.4. The use of heterospecific scent marks

No evidence was obtained for *inter*specific olfactory eavesdropping in *T. corvina*; equal numbers of *T. corvina* foragers visited the food source on which *Melipona beecheii* bees had previously foraged and the control feeder without scent marks. Admittedly, our experiments did not verify the deposition of scent marks by *M. beecheii* foragers. However, the results of pilot experiments indicated *M. beecheii* foragers to deposit and use scent marks in choice experiments (F. Rojas, personal communication). Moreover, *M. beecheii* foragers were occasionally observed to try and revisit the feeding layer they had previously foraged on and that was used for the M-feeder in the choice experiments with *T. corvina*, even though the test feeders were moved far away from the feeder location used to collect scent marks from the *M. beecheii* colony. Together, these observations suggest that the lack of a clear reaction of *T. corvina* foragers to the M-feeder in the current experiment was not due to an absence of *M. beecheii* scent marks.

T. corvina foragers may not have reacted to the *M. beecheii* scent marks because the composition of these heterospecific scent marks was not sufficiently similar to the own scent marks to which they were trained. Alternatively, the test subjects may have lacked the ability to detect *M. beecheii* scent marks. Although *T. corvina* can be categorized as an extirpator species (Johnson, 1983) and dominates *M. beecheii* on artificial food sources (J. Slaa, personal communication), no information is available on the frequency and aggressiveness of encounters between *T. corvina* and *M. beecheii* on food sources under natural circumstances. If *T. corvina* and *M. beecheii* do not have a history of frequent interactions, *T. corvina* may not have evolved the ability to detect *M. beecheii*'s scent marks.

In contrast, *T. spinipes* bees have been reported to strongly prefer a food source scent marked by *M. rufiventris* bees over a clean feeder, whereas *M. rufiventris* foragers showed a strong aversion towards *T. spinipes* scent marks (Nieh et al., 2004b). However, these species were observed to occur on the same natural food sources, with *T. spinipes* harassing and attacking *M. rufiventris* (Nieh et al., 2004b).

It would be interesting to elucidate the exact ecological circumstances under which a stingless bee species' ability to detect and use scent marks deposited by other stingless bee species has evolved. If, in addition, more knowledge would be acquired on the extent to which heterospecific scent marks are used in a natural context by honeybees and bumblebees, we may be able to unravel the phylogeny of this behaviour.

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Résumé – Utilisation des marques odorantes de la source de nourriture par l'abeille sans aiguillon *Trigona corvina* (Hymenoptera : Apidae) : importance de l'identité du dépositaire. Le dépôt et l'utilisation de marques odorantes sur les sources de nourriture ont été trouvées chez les butineuses des abeilles solitaires, des bourdons, des abeilles sans aiguillon et des abeilles domestiques. L'importance de l'identité du dépositaire sur l'utilisation de ces marques odorantes n'a pourtant jamais été systématiquement étudiée chez une même espèce. Le but de cette étude était de déterminer si les butineuses de l'abeille sans aiguillon *Trigona corvina* Cockerell utilisent les marques odorantes déposées par elles-mêmes, par des membres de la colonie, des congénères d'une colonie différente et par des abeilles sans aiguillon d'une autre espèce pour localiser une source de nourriture intéressante. Nous avons offert individuellement à des abeilles *T. corvina* le choix entre deux nourrisseurs test : l'un marqué (M), l'autre non marqué (U) (Fig. 1), qui ne différait du premier que par un élément : la couche de nourriture du nourrisseur M devait contenir des marques odorantes, puisqu'il avait été visité juste avant et de façon répétée par soit (i) le sujet testé, (ii) des membres de la même colonie que le sujet testé, (iii) des congénères d'une autre colonie ou (iv) des abeilles sans aiguillon d'une autre espèce (*Melipona beecheei*). Nous avons enregistré le choix (nourrisseur M ou U) de chaque sujet testé. Nous avons groupé les premiers choix de tous les sujets testés par expérience et déterminé si la distribution des abeilles sur les deux nourrisseurs différait significativement d'une distribution aléatoire.

Les butineuses de *T. corvina* ont significativement préféré le nourrisseur M contenant leurs propres marques odorantes à un nourrisseur témoin propre (test χ^2 : nombre d'abeilles visitant le nourrisseur M vs. le nourrisseur U, $n = 12$, $\chi^2_{0,05,\,1} = 12{,}00$, $P <$ 0,001 ; Fig. 2, 1^{re} colonne). De même, on a observé une préférence significative pour une marque odorante laissée par des membres de la colonie ($n = 17$, $\chi^2_{0,05,\,1} = 13{,}24$, $P < 0{,}001$; Fig. 2, 2^{e} colonne) et par des congénères d'une autre colonie ($n = 28$, $\chi^2_{0,05,\,1} = 5{,}14$, $P = 0{,}023$; Fig. 2, 3^{e} colonne) par rapport au nourrisseur U. Mais nous n'avons pas trouvé de preuve de l'utilisation des marques odorantes déposées par l'autre espèce, *M. beechei* ($n = 18$, $\chi^2_{0,05,\,1} = 0{,}22$, $P = 0{,}637$; Fig. 2, 4^{e} colonne).

L'utilisation des propres marques odorantes a déjà été mentionnée chez diverses espèces d'abeilles sans aiguillon (par ex. Aguilar and Sommeijer, 2001 ; Aguilar et al., 2004a), chez des abeilles solitaires (Gilbert et al., 2001), chez des bourdons (Goulson et al., 1998) et chez des abeilles domestiques (Giurfa, 1993 ; Williams, 1998). Ce comportement a donc pu être présent chez un ancêtre commun à ces quatre tribus. Les propres marques odorantes peuvent être utilisées comme signal d'auto-orientation pour faciliter les revisites à des sources intéressantes et pour éviter de revisiter celles qui sont épuisées. L'attraction par les marques odorantes des membres de la colonie s'observe chez de nombreuses espèces d'abeilles sans aiguillon (par ex. Nieh, 1998 ; Goulson et al., 2001 ; Nieh et al., 2003a, b ; Schmidt et al., 2003 ; Aguilar et al., 2004a ; Hrncir et al., 2004 ; Jarau et al., 2004 ; Nieh et al., 2004a, b ; Schmidt et al., 2005) et chez les abeilles domestiques (von Frisch, 1967 ; Ferguson and Free, 1979 ; Free and Williams, 1983). Elles facilitent probablement le recrutement de butineuses naïves pour des sources de nourriture de grande qualité (Michener, 1974).

La capacité à utiliser les marques odorantes disposées par d'autres colonies de la même espèce ou d'espèces différentes existe aussi chez les abeilles domestiques et les bourdons (Goulson et al., 1998, 2000, 2001 ; Stout and Goulson, 2001 ; Williams, 1998) et chez d'autres espèces d'abeilles sans aiguillon (Villa et Weiss, 1990 ; Nieh et al., 2004b ; Schmidt et al., 2005). L'expression « écouter aux portes de façon olfactive » (Nieh et al., 2004b) décrit peut-être mieux ce comportement. Un plus grand nombre d'études systématiques chez des espèces appartenant à diverses tribus d'abeilles pourrait permettre de mieux débrouiller la fonction et la phylogenèse du comportement de marquage odorant de la source de nourriture.

***Trigona* / abeille sans aiguillon / marque odorante / source de nourriture / communication chimique / Apidae**

Zusammenfassung – Die Wichtigkeit der Identität des Markierenden bei der Nutzung von Geruchsmarkierungen an den Futterquellen durch die Stachellose Biene *Trigona corvina*. Die Anbringung und Nutzung von Geruchsmarken an Futterquellen wurde bei solitären Bienen, Hummeln, Stachellosen Bienen und bei Honigbienen gefunden. Ob hierbei die Identität des die Markierungen anbringenden Tieres von Bedeutung ist, wurde niemals innerhalb der gleichen Bienenart systematisch untersucht. In dieser Untersuchung sollte bestimmt werden, ob Arbeiterinnen der Stachellosen Bienenart *T. corvina* zum Wiederauffinden einer profitablen Futterquelle die von ihnen selbst angebrachten Markierungen, die von Nestgenossen oder von aus anderen Nestern stammenden Arbeiterinnen der gleichen Art nutzen. Wir boten einzelnen *T. corvina* Bienen die Wahl zwischen zwei Testfutterstellen (markiert M und unmarkiert U, Abb. 1), die sich nur darin unterschieden, dass von dem M Fütterer angenommen worden konnte, dass er Geruchsmarken aufwies, da er zuvor mehrfach entweder (1) von dem Versuchssubjekt selbst, (2) von den Nestgenossen des Versuchssubjektes, (3) von Artgenossen aus einem anderen Nest oder (4) von Stachellosen Bienen einer anderen Art (*Melipona beecheii*) besucht worden war. Für jedes Subjekt registrierten wir, ob es den M oder den U Fütterer besuchte. Wir fassten die Erstwahlen aller Testsubjekte in jedem der Experimente zusammen und bestimmten, ob ihre Verteilung auf die Futterstellen von einer Zufallsverteilung signifikant abwich.

Arbeiterinnen von *T. corvina* bevorzugten den ihre eigenen Duftmarkierungen enthaltenden M Fütterer gegenüber einem sauberen Kontrollfütterer (Chi-quadrat-Test, $n = 12$, $\chi^2_{0,05,\,1} = 12{,}00$, $P < 0{,}001$; Abb. 2, erste Kolumne). Eine ähnlich signifikante Präferenz bestand, wenn die Futterstelle von Nestgenossen ($n = 17$, $\chi^2_{0,05,\,1} = 13{,}24$, $P < 0{,}001$; Abb. 2, zweite Kolumne) oder von Bienen der gleichen Art aus einem anderen Volk markiert war ($n = 28$, $\chi^2_{0,05,\,1} = 5{,}14$, $P = 0{,}023$; Abb. 2, dritte Kolumne). Wir fanden aber keine Evidenz für die Nutzung der von anderen Stachellosen Bienen zurückgelassenen Markierungen ($n = 18$, $\chi^2_{0,05,\,1} = 0{,}22$, $P = 0{,}637$; Abb. 2, vierte Kolumne).

Die Nutzung eigener Geruchsmarkierungen an Futterstellen wurde bislang bei mehreren Arten der Stachellosen Bienen (e.g. Aguilar und Sommeijer, 2001; Aguilar et al., 2004a), Solitären Bienen (Gilbert et al., 2001), Hummeln (Goulson et al., 1998) und Honigbienen (Giurfa, 1993; Williams, 1998) festgestellt. Das Verhalten könnte daher bereits bei einem gemeinsamen Vorfahren der vier Bienentribi bestanden haben. Die eigenen Geruchsmarken könnten als Signal zur eigenen Orientierung zum Wiederauffinden profitabler und der Vermeidung bereits geleerter Futterquellen gedient haben.

Die attraktive Wirkung der Duftmarken von Nestgenossen wurde bei vielen verschiedenen Arten der Stachellosen Bienen beobachtet (siehe z.B. Nieh, 1998; Goulson et al., 2001; Nieh et al., 2003a, b; Schmidt et al., 2003; Aguilar et al., 2004a; Hrncir et al., 2004; Jarau et al., 2004; Schmidt et al., 2005), aber auch bei Honigbienen (von Frisch, 1967; Ferguson und Free, 1979; Free und Williams, 1983). Der Geruch der Nestgenossen hilft vermutlich unerfahrenen Sammlerinnen profitable Futterquellen zu rekrutieren (Michener, 1974).

Dagegen kann die Fähigkeit zur Nutzung von Duftmarken von Arbeiterinnen anderer Kolonien der eigenen oder einer anderen Art, wie sie auch bei Honigbienen oder Hummeln (Goulson et al., 1998, 2000, 2001; Stout und Goulson, 2001; Williams, 1998) sowie bei anderen Arten der Stachellosen Bienen (Villa und Weiss, 1990; Nieh et al., 2004b; Schmidt et al., 2005) gefunden wird, am besten als "olfaktorisches Abhören" beschrieben werden (Nieh et al., 2004b). Durch systematische Studien über den Einfluss der Identität des die Markierungen hinterlassenden Tieres auf die Nutzung von Futterquellenmarkierungen bei den einzelnen Arten der verschiedenen Bienentribi könnte es möglich werden, die Details der Funktion und Stammesgeschichte des Futterquellenmarkierens aufzuschlüsseln.

Geruchsmarken / Futterquellen / Marker / Stachellose Bienen / *Trigona* / Apidae

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