

Honeybee recruitment to scented food sources: correlations between in-hive social interactions and foraging decisions

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Received: 6 July 2011 / Revised: 28 October 2011 / Accepted: 28 October 2011 / Published online: 15 November 2011
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Abstract Information exchange of environmental cues facilitates decision-making processes among members of insect societies. In honeybee foraging, it is unknown how the odor cues of a resource are relayed to inactive nest mates to enable resource exploitation at specific scented sources. It is presumed that bees need to follow the dance or to be involved in trophallaxis with a successful forager to obtain the discovered floral scent. With this in mind, we evaluated the influence of food scent relayed through in-hive interactions and the subsequent food choices. Results obtained from five colonies demonstrated that bees arriving at a feeding area preferred to land at a feeder carrying the odor currently exploited by the trained forager. The bees that landed at this feeder also showed more in-hive encounters with the trained forager than the individuals that landed at the alternative scented feeder. The most frequent interactions before landing at the *correct* feeder were body contacts with the active forager, a behavior that involves neither dance following nor trophallaxis. In

addition, a reasonable proportion of successful newcomers showed no conspicuous interactions with the active forager. Results suggest that different sources of information can be integrated inside the hive to establish an odor-rewarded association useful to direct honeybees to a feeding site. For example, simple contacts with foragers or food exchanges with non-active foragers seem to be enough to choose a feeding site that carries the same scent collected by the focal forager.

Keywords Social interactions · Decision making · Communication · Foraging · Honeybee · *Apis mellifera*

Introduction

Honeybee, *Apis mellifera*, foraging efficiency at the individual level can be understood as the trade-off between optimizing crop loading behavior at a food source and exchanging food-related information inside the hive (Núñez 1982). However, the coordination to perform foraging at the social scale is based on the use of different and complex communication mechanisms displayed in and outside the nest, including the transmission of location information, the assessment of food source profitability, and the memorization of specific characteristics of the discovered resource, such as its floral scent (see von Frisch 1967; Seeley 1995; Grüter and Farina 2009).

While the dance of the honeybee indicates the area of the profitable food source (von Frisch 1967; Riley et al. 2005), the presence of other bees flying around the feeding site (Tautz and Sandeman 2003) and the release of recruiting pheromones (Pflumm 1969) are also important to guide short-range searching (von Frisch 1923; Johnson and Wenner 1966). Also, the floral scent information of the

Communicated by R. Moritz

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discovered resource is highly relevant within this context because it can be transferred within the hive (von Frisch 1923, 1967; Johnson and Wenner 1966; Ribbands 1954; Free 1969; Arenas et al. 2007, 2008). The use of floral scent as a guiding cue to find the feeding site implies the establishment of odor-rewarded memories inside the colony (Farina et al. 2005), in which the mouth-to-mouth trophallaxis among nest mates would be the most plausible underlying mechanism (Gil and De Marco 2005; Farina et al. 2007). However, odor particles carried on the forager's body surface seem to be sufficient stimuli for foraging activation in some cases (von Frisch 1923). It has been reported that during foraging, dance following and trophallaxis are the most common interactions between active foragers and hive bees. However, it has also been observed that many bees are still able to arrive at the food source even without any contact with the active foragers inside the nest (Gil and Farina 2002). In this sense, it seems that not all bees require the same stimulation before foraging activation, a fact related to the field experience of these individuals (Gil and Farina 2002; Fernández et al. 2003).

Until now there has been no evidence about what controls the final approach and landing of recruits to scented food sources. To approach this, it is relevant to determine how information about naturally scented resources is transmitted to activate foraging. In this respect, the impact of different in-hive interactions on foraging decisions between scented feeding sites is still unknown. Although it has been suggested that trophallaxis with the incoming forager would be relevant to foraging activation (Farina et al. 2005, 2007; Grüter et al. 2006), there is no direct evidence about what kind of social interactions occurring within the hive cause a biased preference at a feeding site. In this study, the landing choices of previously marked honeybees were evaluated after they were observed interacting with a focal forager inside the nest. The focal forager could have collected either a scented or unscented sucrose solution from the training feeder. The preferences of the marked bees were tested at the foraging site after the training feeder was covered, hence not accessible for these individuals, and two additional scented feeders (testing feeders) were offered instead. Thus, we analyzed the scent choice at the feeding site together with the occurrence of interactions inside the hive with focal foragers during the moments before the marked bees arrived at one of the testing feeders.

Material and methods

Five colonies with 3,000–3,500 *A. mellifera* L. honeybees each were housed in two-frame observation hives. Colonies had a queen, brood, and reserves. The experiments were

carried out in three observation hives from February to April in 2008 (H1–H3) and in two observation hives in 2009 (H4 and H5) at the experimental field of the University of Buenos Aires. We used one hive at a time to perform the experiments.

Experiment procedure

Approximately 70–100 bees were trained to collect an unscented 50% weight/weight (*w/w*) sucrose solution at an ad libitum training feeder (feeder 0, F0) located 110 m from the observation hive. The training consisted of the presentation of an artificial feeder containing unscented sucrose solution at the hive entrance. Once a group of bees were feeding from it, the feeder was moved a short distance away from the original site. Once these bees returned, the procedure was repeated until the final feeding location was reached (von Frisch 1967). During the training period, foraging bees were numbered with plastic tags (Opalithplättchen) on the thorax for individual identification (marked bees).

The experiment took place during three consecutive days (unscented situation, days 1 and 2; scented situation, day 3). Before starting the measurements (testing period), unscented sucrose solution 50% *w/w* was offered from 10:00 to 11:00 at F0 (training period). During this period, the marked bees confirmed that the food source was still available. Thereafter, from 11:00 to 14:00, the feeder used during the training period (F0) was depleted, cleaned, and maintained in the same location until the beginning of the testing period.

Unscented situation (days 1 and 2)

From 14:00 to 15:00, F0 was refilled with 50% *w/w* unscented sucrose solution and two additional feeders (testing feeders), feeder 1 (F1) and feeder 2 (F2), were located equidistant from F0 (Fig. 1) The testing period began once a single experienced forager (henceforth focal forager) returned to F0, while the remainder of the (marked) bees had access only to F1 or F2, which offered scented sucrose solution but at a lower concentration (18% *w/w*). The use of a diluted sucrose solution allowed bees to land at one of these feeders and begin to ingest, a situation that facilitated the capture of all the bees that arrived at the feeding area.

The testing feeders, F1 and F2, were scented with two glass Petri dishes (1 cm high, 15 cm in diameter) containing a paper filter disk (55 mm in diameter) soaked with a pure scent (50 μ l essential oil) placed below each feeder (Arenas et al. 2007). The scents used on F1 and F2 during the first testing day were inverted on day 2 (Fig. 1, left and center panel). During days 1 and 2, the sucrose solution offered on F0 was unscented (*unscented situation*).

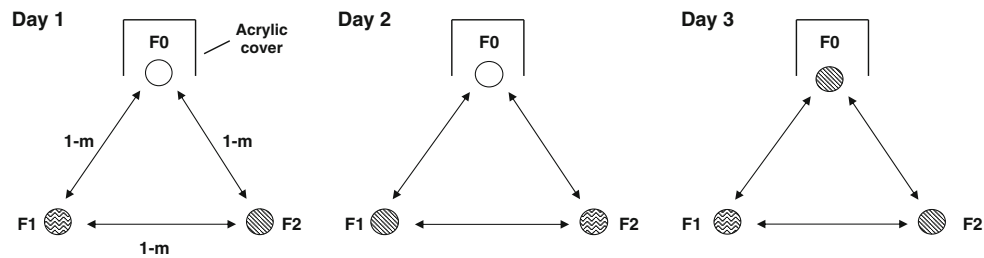


Fig. 1 Experimental foraging device during the testing phase. Three feeders were offered simultaneously 110 m from the colony: F0 was the feeder in which only the trained focal forager had access. This was possible by covering it with an acrylic cylindrical dome while the bee fed. The alternative feeders, F1 and F2, were scented (*fill patterns*) and freely accessible to the marked bees, which were captured

During the testing period, only the focal forager had access to F0. This was possible since F0 was covered with an acrylic cylindrical dome (15 cm diameter, 15 cm high) while the focal forager ingested sucrose solution. Thus, the marked bees had foraging experience in this surrounding but could not land on this feeder and had to choose between the alternative feeders, F1 and F2, where they were captured immediately and eliminated in order to avoid being double counted and carrying the scent into the hive. Then, we recorded the behavioral interactions that occurred inside the colony between the focal forager and the marked hive bees by using a video camera (DCR-TRV 310 and Sony Handycam HDR-SR11). The observer at the feeders and the observers at the laboratory maintained direct contact using walkie-talkies.

Scented situation (day 3)

The procedure used on this day was the same used during the unscented situation (days 1 and 2), but unlike on those days, F0 was *scented* with the scent (50 μ l essential oil per liter of sugar solution) that was less preferred by the bees in previous testing days (unscented situation) (Fig. 1, right panel).

To scent F1 and F2 during the three experimental days and F0 during the third day, we used five pairs of scented synthetic mixes, one pair for each hive: H1: rose–vanilla, H2: mandarin–sandal, H3: bergamot–strawberry, H4: cypress–tea tree, and H5: peach–lemongrass.

The food scent entered the hive for the first time when the focal forager collected scented sugar solution at F0 during day 3 (scented situation). Only through the focal forager could the rest of the hive mates have access to the food scent.

Behavioral observations

We quantified different categories of interactions between the focal forager and the hive bees, which had been individually numbered in previous feeding bouts at F0 (marked bees). We defined the following categories of

interactions immediately after landing. During days 1 and 2, food-choice behavior was analyzed by comparing landings at F1 and F2, while the trained focal forager was fed an unscented solution at F0. During day 3, the less-preferred location during days 1 and 2 was chosen as the feeder location that offered the scent collected by the trained focal forager from F0

interaction between the focal forager and marked bees inside the hive (Gil and Farina 2002): (1) no contact (NC), no body contact between the marked bees and the focal forager; (2) body contact with the focal forager (BC), the marked bee touched the body of the focal forager without following dance; (3) trophallaxis (TRF), the marked bee touched the mouth parts of the focal forager with its protruded proboscis without following dance; (4) follow dance (FD), the marked bee followed the dance maneuvers performed by the focal forager; (5) trophallaxis and follow dance (TRF&FD), the marked bee followed the dance and also had trophallaxis with the focal forager.

All of the categories defined above were mutually exclusive. Since during the experimental period marked bees could interact with the focal forager in more than one of the hive stays (i.e., permanencies inside the hive in-between foraging bouts), the type of interaction was related to the experimental period. At the same time, on the feeders, we recorded the time and the number of marked bees that landed at each feeder.

Statistical analysis

Fisher's exact tests were performed to compare the proportions of bees that landed at one of the testing feeders (F1 or F2) per colony, while a heterogeneity chi-square analysis was used to test the same variable after pooling data of the five hives after a correction for continuity (Zar 1999).

For a global analysis between treatments, the type of interaction that occurred inside the hive, and the feeder chosen, we used a generalized linear mixed-effects model (GLMM) in R v 2.9 (R Development Core Team 2009). R fitted the models with the lmer function (Bates 2007). We used the type of social interaction and treatment (unscented and scented situation) as fixed effects; we included the colony as a random effect to control for the non-independence of data points from the same colony. We examined the significance of the fixed effects using Wald tests (Bolker et al. 2009; Zuur et al. 2009).

To compare the proportion of the bees that arrived at the feeders according to the number of forager's hive stays with interactions for both experimental situations, a new GLMM test was also performed (R v 2.9, R Development Core Team 2009). R fitted the models with the lmer function (Bates 2007). We used HS (hive stays) and treatment as fixed effects.

Results

During days 1 and 2, the food-choice behavior of the marked bees was analyzed by comparing landings at both experimental feeders, F1 and F2, while the focal forager fed on the unscented solution at F0. On day 3, the less-preferred testing feeder during days 1 and 2 (F2) was chosen as the site that offered the scent collected by the focal forager at F0 during the scented situation (Fig. 1). Thus, by comparing the proportion of arrivals at F2 for both experimental situations, statistical analysis performed for each colony showed that more bees preferred to land on F2 when F0 was scented compared to when F0 was unscented (contingency table, 2×2 ; Fisher's exact test, H1, $\chi^2=7.59$, $df=1$, $P=0.0059$; H2, $\chi^2=16.39$, $df=1$, $P=0.0001$; H3, $\chi^2=2.4$, $df=1$, $P=0.1211$; H4, $\chi^2=2.2$, $df=1$, $P=0.1382$; and H5, $\chi^2=3.92$, $df=1$, $P=0.04$; Fig. 2). The five colonies showed a similar response pattern when the proportion of marked bees landed at the experimental feeder F2 was analyzed under both experimental situations (heterogeneity test: $\chi^2=0.47$, $df=4$, $P=0.976$). We then

pooled the data relating to all the colonies and still found significant differences for both situations, with or without the scented solution at F0 (Yates correction: $\chi^2=30.65$, $P<0.005$, see inserted figure in Fig. 2). Thus, marked bees preferred to land on the feeding site offering the same scent exploited by the trained focal forager.

Using GLMM, we analyzed the experimental situation and the type of social interaction in relation to the bees' choice of experimental feeder (Fig. 3). The experimental situation effect was significant (GLMM, $z=3.39$, $P=0.0007$), indicating that more bees landed on F1 when the unscented sugar solution was offered at F0. Under the unscented situation, the type of interaction effect was not significant (for details see GLMM presented in Fig. 3). However, significant differences were found between no contact and body contact for the scented situation, although not for the rest of the comparisons (see GLMM in Fig. 3). This result suggests that at least some kind of interaction between the focal forager and the marked bees within the hive would be needed to land at the "correct" feeder, i.e., F2.

The number of permanencies of the focal forager inside the nest in-between foraging bouts (henceforth hive stay) that involved social interactions with bees that arrived later at one of the experimental feeders was also recorded (Fig. 4). We found significant differences between treatments (GLMM, $z=4.605$, $P<0.005$) and between the number of hive stays with social interactions (i.e., one hive stay with interactions, HS1, vs hive stays without interactions, HS0: $z=2.198$, $P=0.023$; GLMM). For the unscented situation, we

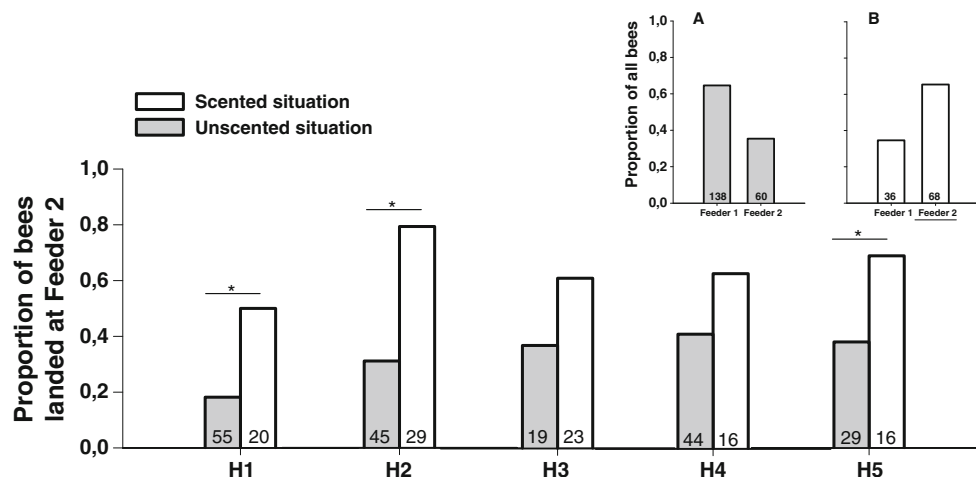


Fig. 2 Arrivals of the experienced foragers under the scented/unscented situation. The proportion of bees that landed at F2 (the feeder that offered the same scent of the food collected by the trained focal forager at F0 during the scented situation). Individuals were captured once they landed on F1 and F2 while the trained focal forager fed on F0 under either the unscented situation (gray bars) or scented situation (white bars). H1, H2, H3, H4, and H5 represent the beehives used during the experiment. The number of bees landing on F2 is shown at the bottom of each bar. Asterisks indicate statistical

differences in Fisher tests ($*P<0.05$; see "Results" for details). *Insert:* Proportion of the total marked bees that landed and were captured in each testing feeder (bees of the five colonies were pooled) while the trained focal forager collected under the unscented (a) or scented situation (b) on F0. The number of bees landing on F1 and F2 is shown at the bottom of each bar. Asterisks indicate statistical differences in Fisher tests ($*P<0.05$; see "Results" for details). F2 is underlined in the scented situation (b), indicating that it offered the same scent as F0

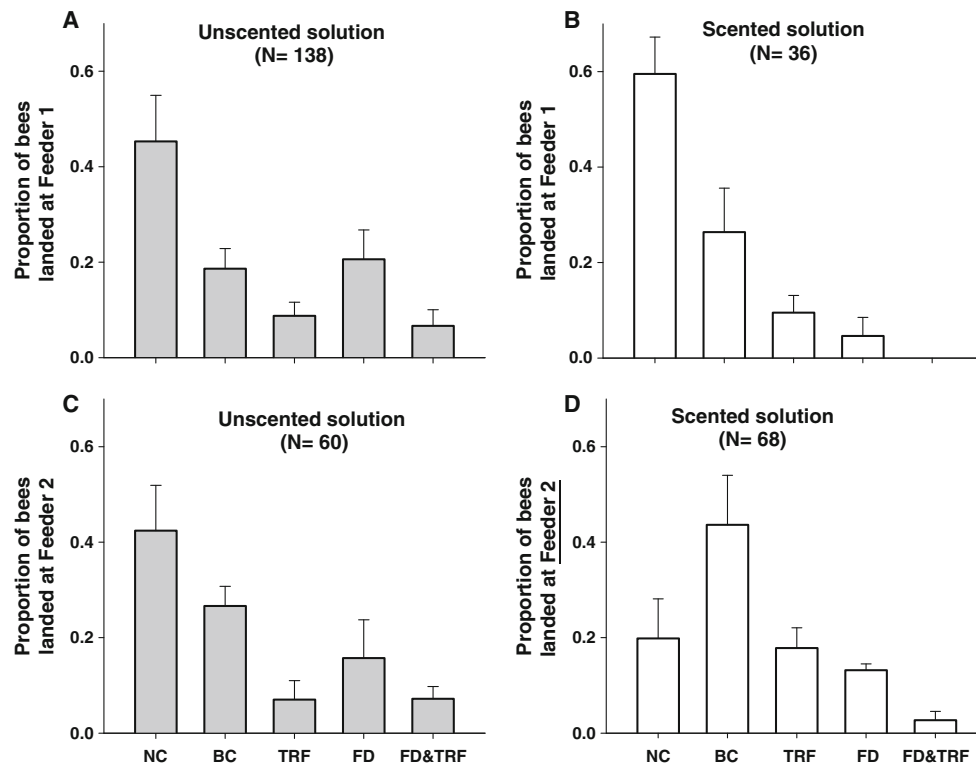


Fig. 3 Distribution of in-hive social interactions under the scented/unscented situation. The proportion of the total experienced marked bees (means \pm SE) captured once they had landed on the F1 (**a** and **b**) and F2 (**c** and **d**). Results were pooled according to the category of the interaction they performed with the trained focal forager inside the nest and under both experimental situations, i.e., the trained focal forager collected at F0 either unscented food (*gray bars*, **a** and **c**; GLMM for unscented situation: no contact vs. body contact: $z=0.4$, $P=0.68$; NC vs. trophallaxis, TRF: $z=0.11$, $P=0.91$; NC vs. follow dance: $z=0.53$, $P=0.59$; NC vs. FD&TRF: $z=-0.32$, $P=0.75$; BC vs. TRF: $z=-0.32$, $P=0.75$; BC vs. FD: $z=0.14$, $P=0.89$; BC vs. FD&TRF: $z=-0.53$, $P=0.59$; TRF vs. FD: $z=0.39$, $P=0.69$; TRF vs.

FD&TRF: $z=-0.16$, $P=0.88$; FD vs. FD&TRF: $z=-0.6$, $P=0.55$) or scented food (*white bars*, **b** and **d**; GLMM for scented situation: NC vs. BC: $z=2.27$, $P=0.023$; NC vs. TRF: $z=1.64$, $P=0.10$; NC vs. FD: $z=1.57$, $P=0.12$; BC vs. TRF: $z=0.22$, $P=0.83$; BC vs. FD: $z=0.44$, $P=0.66$; TRF vs. FD: $z=0.23$, $P=0.82$). F2 is underlined in the scented situation (**d**), indicating that it offered the same scent as in F0. NC indicates no contact; BC indicates touching the body of the focal forager; TRF indicates trophallaxis was performed; FD indicates the following of dances only; FD&TRF indicates the following of dances and performing trophallaxis even within the same hive stay. All of the categories defined were mutually exclusive. The number of bees landing on each feeder is shown in *parenthesis*

did not find significant differences between the proportion of arrivals to F1 and F2 and the number of the focal forager's hive stays with interactions [Fig. 4a; GLMM: HS0 vs. HS1: $z=0.775$, $P=0.438$; HS0 vs. HS2 (two hive stays with interactions): $z=-0.414$, $P=0.679$; HS0 vs. HS3 (three hive stays with interactions): $z=1.008$, $P=0.313$; HS0 vs. HS4 (four hive stays with interactions): $z=-0.009$, $P=0.993$]. In contrast, for the scented situation, the distribution of arrivals significantly differed depending on the feeder the marked bees chose, showing a higher number of hive stays before departure to the feeder that presented the same scent exploited by the focal forager (F2) (Fig. 4b; GLMM test: HS0 vs. HS1: $z=2.870$, $P=0.0041$; HS0 vs. HS2: $z=1.92$, $P=0.055$; HS0 vs. HS3: $z=0.668$, $P=0.504$; HS0 vs. HS4: $z=0.01$, $P=0.992$). In other words, the bees that arrived at the “correct” feeder seemed to need more encounters with the focal forager. Matching this finding, those bees that landed at the feeder with the novel scent (F1, scented situation) also had shorter delays

compared with those that arrived at the F2 feeder offering the exploited scent (mean delay for F1 was 18.7 min and 23.5 min for F2).

Under both experimental situations, around 40% of the bees that arrived at the feeding area showed no conspicuous interaction with the focal forager (Fig. 4a and b) and also showed no significant differences between the unscented and the scented situation for the “no contact” category, NC (Fisher's exact test: $\chi^2=1.76$, $df=1$, $P=0.1845$). Therefore, if we considered the bees that arrived at one of the experimental feeders after interacting with the focal forager during only a single hive stay of the focal forager, we found that the food choices at the feeding device depended on the experimental situation. For the unscented situation, the type of in-hive interaction that occurred immediately before arriving at one of the feeders was similar and independent of the food choice (Fig. 5a; test for independence: $\chi^2=1.166$, $df=3$, $P=0.761$). This was not the case for the scented situation, in which we observed higher proportions

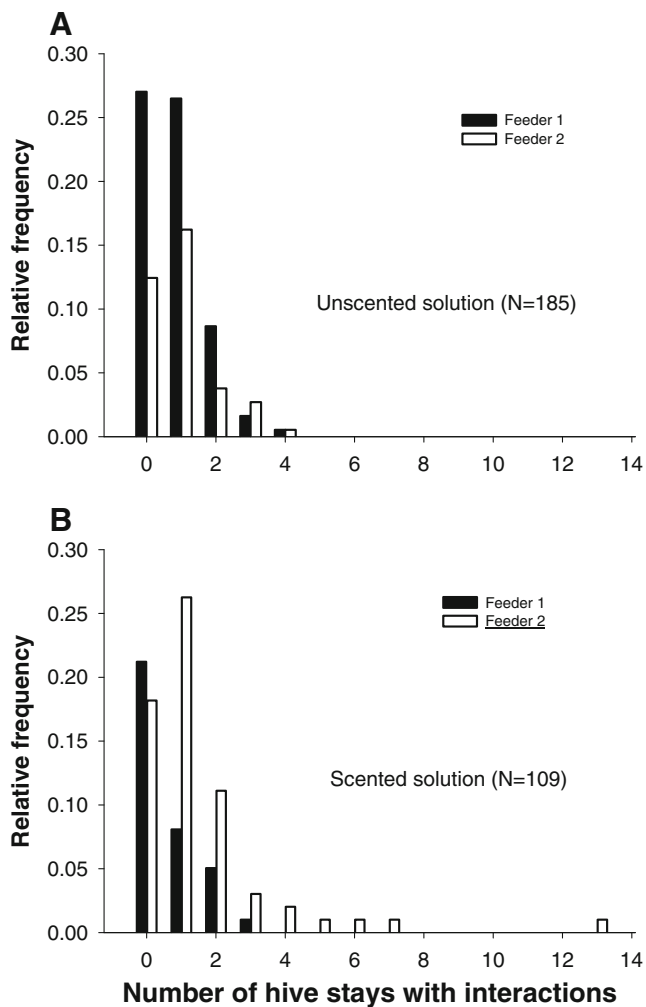


Fig. 4 Number of hive stays (permanencies inside the hive in-between foraging bouts) with social interactions before arriving at the scented or unscented feeding site. The number of marked bees, expressed in relative frequencies, that landed at the F1 (black and white bars) or F2 (white bars) after a number of hive stays in which the experienced marked bee interacted with the trained focal forager. F0 offered unscented sucrose solution during days 1 and 2 (a) and scented sucrose solution during day 3, (b). The number of bees landing on each feeder is shown in *parenthesis*. F2 is underlined in the scented situation (b), indicating that it offered the same scent as F0

of any social interactions before departure to the “correct” F2 feeder (Fig. 5b; no statistical analysis was made here due to the absence of data in some categories, Zar 1999).

Discussion

In this study, we investigated social interaction factors that impact on honeybee foraging decisions between scented food sources. Our main finding is that individuals that have any type of social interactions are more likely to forage at a feeding site with the same scent as the resource collected by the focal forager. These interactions do not necessarily have

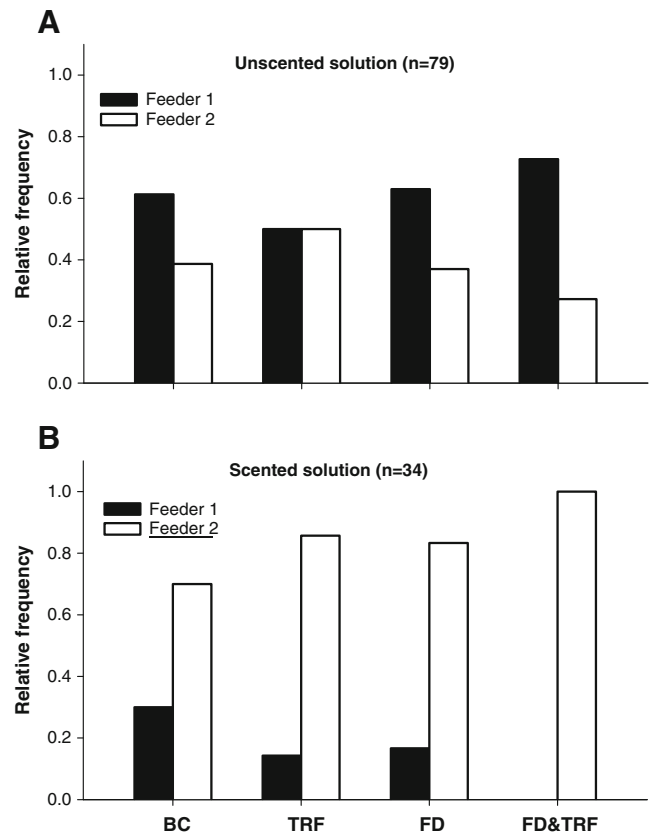


Fig. 5 Social interactions that occurred just before arriving at one of the experimental feeders. Categories of social interactions between the bees that arrived and the trained focal forager before landing at one of the experimental feeders under the unscented situation (a) and the scented situation (b). The in-hive interactions considered occurred only after one hive stay of the trained focal forager. Black bars F1, white bars F2. The number of bees landing on each feeder is shown in *parenthesis*. F2 is underlined in the scented situation (b), indicating that it offered the same scent as F0

to be dance following or trophallaxis; they can be simple body contacts.

Coincidentally with previous studies (von Frisch 1923, 1967; Johnson and Wenner 1966; Ribbands 1954; Free 1969; Arenas et al. 2007, 2008), we found that honeybees preferentially chose a feeding site that had the same scent collected by a nest mate (the focal forager), under our experimental conditions. Having corroborated this, we went further and quantified the different social interactions in which the bees were involved before landing at the *correct* feeder (i.e., a novel feeder that offered the same scent collected by the focal forager located close to the trained feeder). We found that these bees performed more interactions inside the colony with the focal forager than the bees that had arrived at the alternative feeder. Their most frequent interactions were contact with the body of the focal forager, a behavioral category that involved neither dance following nor trophallaxis. Thus, floral scent perceived by *simple* social interactions seems to provide

enough information to bias the food choice behavior of marked bees in the area immediately surrounding the feeding site. This finding comes as a consequence of having quantified *in-hive social* interactions of recruited bees in this context for the first time.

This experiment allowed us to analyze the first food choice of the marked bees visiting a scented feeding site as well as reducing the interference of sensory cues in the foraging surroundings such as the presence of active foragers, which can affect landing decisions (Tautz and Sandeman 2003). The bees that arrived had previously collected unscented food in the training feeder, but the presence of scent in the foraging context was a new situation that forced these subjects to choose one of the scented test feeders. Results show that in all of the five colonies tested, the marked bees mainly landed at the *correct* feeder (F2) during the scented situation (Fig. 2).

After these biased responses, the question about what controls the final approach and landing at scented food sources is worth considering. For this, we correlated the arrivals at the food source of marked bees with their recent *in-hive* experiences. In this sense, it has been suggested that trophallaxis with an active foraging honeybee is necessary to activate the search for scented food sources (Farina et al. 2005, 2007; Grüter et al. 2006; Arenas et al. 2007, 2008). However, only one eusocial insect study showed the role of trophallaxis to transfer food scent information and its later use at the foraging context. In the study, carpenter ants, *Camponotus mus*, involved in nectar-exchange trophallaxis events showed biased behavior toward a feeder scented with the food odor transferred via oral contact by an active foraging ant, showing a clear role of this information while ants orientate toward an appetitive goal (Provecho and Josens 2009). Moreover, the ants that were not engaged in a trophallaxis but might have perceived the food odor carried by the potential donor (i.e., contacted the body of the nectar-carrying ant without exchanging food) chose the feeder that offered the alternative (novel) scent, suggesting that under these circumstances, an olfactory memory can also be established.

We approached this issue by focusing on the social interactions that occurred within the beehive while a single member of its colony collected a controlled reward. By analyzing the behavior inside the hive according to the later choice at the feeding site, we showed a similar proportion of interactions in both groups arriving at F1 or F2 for the unscented situation (Fig. 3). More than 40% of the bees that landed at the food-choice device showed no interaction with the employed forager (NC) under this experimental situation, a fact reported as common in foraging honeybees with experience in the field (de Vries and Biesmeijer 1998; Gil and Farina 2002; Fernández et al. 2003). In addition, social interactions like body contacts without following dance (BC) were as frequent as the following of dances alone (FD),

while trophallaxis events with the active forager (TRF) were less frequent under the unscented situation.

When the training feeder F0 was scented, the proportion of the *in-hive* interactions significantly differed according to the chosen feeder (Fig. 3). While 60% of the marked bees arriving at the feeder carrying the novel scent performed no conspicuous interaction with the focal forager (NC), the same behavioral category was sharply reduced (20%) in those bees arriving at the *correct* feeder. The most frequent behavioral category for this group was to touch the body of the focal forager without following dance (BC), a proportion that was almost twice that achieved by the bees that arrived at the *wrong* feeder. Also, the occurrence of trophallaxis events (TRF) increased compared with other conspicuous interactions during the scented situation, in contrast with the proportions observed under the unscented situation.

At least one hive stay seems to be enough to increase the proportion of successful arrivals at the feeding site. In addition, the landings at the alternative feeder (i.e., offering the novel scent) could be reduced with more encounters with the focal foragers (Fig. 4). A more detailed analysis after a single forager's hive stay shows that the efficiency of touching the body of the incoming forager achieved a value of 70%, while dance following and trophallaxis improved this efficiency, reaching more than 80% of BCs (Fig. 5). It is clear then that some types of direct scent-mediated interactions between employed and unemployed foragers were relevant to achieve a successful food choice. However, most of the bees that arrived at the correct feeder had neither followed dances nor exchanged food via trophallaxis with the focal forager. A considerable percentage of arrivals also did not show conspicuous interactions with the focal forager (20%; Figs. 3, 4, and 5). Despite this situation and even in the cases in which we did not record any interaction (NC), it is possible that many *correct* arrivals might have been the consequence of receiving the scented food from other hive mates—not the focal forager. If that were the case, the circulation of the scented nectar among bees placed in the dance/delivery area would allow olfactory memory to be established anyway. It is well known that olfactory information can be rapidly propagated inside the hive (Grüter et al. 2006, Ramirez et al. 2010). That, together with the presence of dance-vibrated signals transmitted through the wax comb (Tautz 1996) and the release of active chemicals produced by the dancers (Thom et al. 2007), would be enough to recall learned flight vectors (Johnson 1967, Reinhard et al. 2004, Grüter et al. 2006). Once in the area of the known foraging site, the *in-hive* learned scent would facilitate finding the location of the goal. For novel food sources, the communicated vectors via waggle dance, together with the food scent brought to the hive by the scout, might allow not only the decoding of the new feeding location (von Frisch 1967; Riley et al. 2005; Menzel et al. 2011), but also affect arousal levels

to reactive bees into foraging mode (von Frisch 1923). Thus, within a motivated behavioral context such as dance maneuvers, the dance-following bees might learn the scent carried (von Frisch 1967; Díaz et al. 2007), even without receiving a drop of scented nectar from the successful forager. Therefore, social interactions that may or may not involve *direct* contacts with the active forager would allow the orientation of newcomers toward a profitable food source to be improved, a fact that implies obtaining in-hive information from different sources such as dance vectors, scented foods, vibrated combs, scent of the dancers, among others. Thus, under the absence of conspicuous cues or signals in the surroundings of the feeding site, the presence of incidental cues previously experienced within the social context might contribute to choosing a profitable and predictable resource.

Acknowledgments We are indebted to Christoph Grüter for helping us with the statistical analysis. We are also grateful to Roxana Josens, Andrés Arenas, and Lucila Herbert for valuable comments of the early version of this manuscript. We are also indebted to the two anonymous referees for their valuable comments and suggestions on an early version of this manuscript.

Funding This study was partly supported by grants from ANPCYT (PICT 2010 0425), University of Buenos Aires, CONICET (PIP 112-200801-00150), and Guggenheim fellowship to WMF. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Ethical standards The experiments comply with the “Principles of animal care,” publication no. 86–23, revised 1985 of the National Institute of Health, and also with the current laws of the country in which the experiments were performed. The experiments comply with the current laws of the country in which they were performed.

Competing interests The authors declare that they have no conflict of interest.

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