ORIGINAL PAPER

How floral odours are learned inside the bumblebee (*Bombus terrestris*) nest

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Abstract Recruitment in social insects often involves not only inducing nestmates to leave the nest, but also communicating crucial information about finding profitable food sources. Although bumblebees transmit chemosensory information (floral scent), the transmission mechanism is unknown as mouth-to-mouth fluid transfer (as in honeybees) does not occur. Because recruiting bumblebees release a pheromone in the nest that triggers foraging in previously inactive workers, we tested whether this pheromone helps workers learn currently rewarding floral odours, as found in food social learning in rats. We exposed colonies to artificial recruitment pheromone, paired with anise scent. The pheromone did not facilitate learning of floral scent. However, we found that releasing floral scent in the air of the colony was sufficient to trigger learning and that learning performance was improved when the chemosensory cue was provided in the nectar in honeypots; probably because it guarantees a tighter link between scent and reward, and possibly because gustatory cues are involved in addition to olfaction. Scent learning was maximal when anise-scented nectar was brought into the nest by demonstrator foragers, suggesting that previously unidentified cues provided by successful foragers play an important role in nestmates learning new floral odours.

Keywords Floral scent · Foraging recruitment pheromone · Honeypot · Memory · Social learning

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Introduction

Solitary foraging can be costly in terms of time spent searching for food in unprofitable locations, and reduced efficiency at exploiting a food source compared to group foraging (Clark and Mangel 1986). One way in which social animals can ameliorate these potential costs is by recruitment, i.e. the process by which successful foragers inform other individuals of food availability and solicit them to forage. Cues can help recruited individuals locate a food source, e.g. by observing the feeding activity of other individuals (local enhancement: Leadbeater and Chittka 2007). However, recruitment can be made more efficient by the intentional transmission of information (signals) about the nature of the food source and/or its location, e.g. trail laying in naked mole rats (Judd and Sherman 1996) and ants (Hölldobler and Wilson 1970) or feeding calls in marmosets (Heltne et al. 1981). Recruitment to a newly discovered food source allows animals to effectively exploit patchy resources and reduces the time individuals spend searching for food (Dornhaus et al. 2006).

In honeybees, successful foragers provide direction and distance information for currently rewarding flower patches using the waggle dance (von Frisch 1967) and also transmit information about floral scent (von Frisch 1923; Wenner et al. 1969). Honeybees detect the scents of flower species visited both from the airborne odours associated with the successful forager and also from the nectar transferred by the forager to receiver bees in the nest by trophallaxis (i.e. mouth-to-mouth transfer of regurgitated nutritional fluids; Farina et al. 2005). In contrast, bumblebee foragers cannot communicate geographical information about rewarding food sources, but they can provide odour information from rewarding flower species to their nestmates. Indeed, recruited workers forage preferentially on flowers with the

same odour as the ones from which successful foragers have been collecting nectar (Dornhaus and Chittka 1999).

Recruiting bumblebees release a pheromone that induces non-foraging workers to leave the nest in search of food (Dornhaus et al. 2003). Because this pheromone is released when the successful forager brings the rewarding floral scent into the nest, it could play an essential role in odour learning, paralleling a phenomenon of social learning previously shown in rats (Leadbeater and Chittka 2007). Galef and Wigmore (1983) let a naïve rat interact with a demonstrator rat that had eaten food type A. Then, when given the choice between two novel food types (A and B), the naïve rat always chose food type A that it had previously smelled on the demonstrator's breath. This effect is due to a semiochemical (carbon disulphite) which, when presented in conjunction with food type (i.e. in the absence of a demonstrator rat), elicits a preference for that food type in naïve rats (Galef et al. 1988). A similar phenomenon could occur in bumblebees if the recruitment pheromone acts in the same way as carbon disulphite in rat social learning. The occurrence of a novel floral odour in conjunction with the recruitment pheromone could thus elicit a foraging preference for that specific floral odour. This hypothesis is supported by the fact that pheromones can have an effect on learning behaviour in honeybees, e.g. the queen pheromone appears to prevent aversive learning in young workers (Vergoz et al. 2007). In addition, learning of floral odour does occur inside the nest. For example, exposing young honeybee workers to a floral odour in the nest makes them more likely to forage preferentially on that flower type later in their life (Arenas et al. 2007). The establishment of foraging preferences might thus be conditioned by the presence of recruitment pheromone in bumblebees.

Moreover, how bumblebees transmit information about rewarding floral odours from successful foragers to nest-mates is unknown. The scent brought into the nest by successful foragers could either be transmitted directly through the air or indirectly from the nectar deposited in honeypots, thus potentially involving both olfaction and gustation. In addition, the presence of a recruiting bumble-bee may also facilitate learning, for instance, through behavioural interactions between naïve workers and the recruiting bumblebee, which performs excited runs in the nest during which it bumps into and climbs over nestmates (Dornhaus and Chittka 2001).

In order to assess the mechanisms that underlie floral odour learning in bumblebees, we exposed colonies to a novel scent (either airborne scent, scented sucrose in honeypot or scented sucrose brought in by a forager) in the presence and absence of artificial foraging recruitment pheromone. The foraging preferences of workers were then tested to assess how well they had learned the novel scent

depending on the mode of scent exposure and the presence (or absence) of recruitment pheromone.

Materials and methods

We used four queenright *Bombus terrestris dalmatinus* (Dalla Torre) colonies, supplied by Syngenta Bioline Bees (Weert, The Netherlands). They were each housed in a bi-partite wooden nest box ($28 \times 16 \times 11$ cm) connected to a foraging arena ($116 \times 71 \times 31$ cm) via a transparent Plexiglas tube. Bees were pre-trained to forage from an array of ten artificial flowers in the arena (Fig. 1). Each flower consisted of a blue plastic square (25×25 mm; Perspex® Blue 727), with a small well in the centre, placed on a vertical glass cylinder (diameter=10 mm; height=40 mm). We chose blue because bumblebees are naturally attracted to this colour (Raine et al. 2006), which, therefore, increased the speed with which they learn to forage on the artificial flowers during pre-training. Each flower well was filled with 50 μL of 50% sucrose solution (v/v) and replenished using a micropipette as soon as the solution was consumed and the bee had left the flower. Foragers that fed on the artificial flowers were caught and a unique numbered tag (Opalith Plättchen, Christian Graze KG, Germany) was attached to their thorax so that individual foraging activity could be monitored. Only individuals that resumed foraging after being tagged were used in the experiment to ensure there were only highly active nectar foragers during the test phase. Colonies were fed defrosted honeybee-collected pollen (Koppert B.V., Berkel en Rodenrijs, The Nether-lands), which was added directly to the nest every other day after experiments had ceased.

The experiments consisted of testing the relative preference of foragers for anise over peppermint scents, depending on the way the colony had been exposed to the anise scent
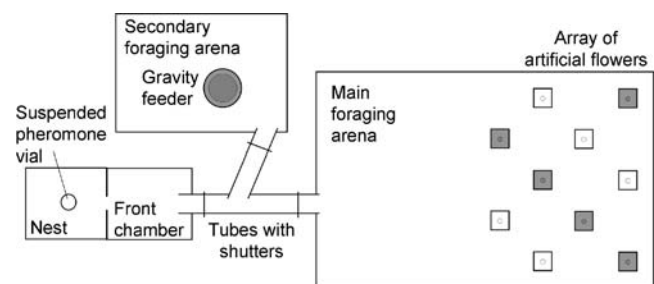
Fig. 1 Schematic aerial view of the experimental setup for foraging preference based on floral scent. Colours on the diagram indicate which flowers contained anise-scented (*grey*) or peppermint-scented (*white*) water solution during the test phases. The secondary arena was only connected to the nest box for treatment 3 (Table 1) so that live 'demonstrator' foragers could collect anise-scented sucrose solution from an ad libitum gravity feeder and bring it back to the nest

and on whether it had received artificial recruitment pheromone. As workers showed an innate preference for peppermint when given the choice between anise and peppermint (see the "Results" section), we chose to investigate learning of the less-preferred scent (anise) to provide a greater range for potential improvement in preference. Seven different treatments were tested (Table 1). The anise scent could enter the colony in three ways. In treatment 1a, anise odour evaporated from a glass vial suspended above the nest through a cotton roll wick (DE Healthcare Products, Gillingham, UK). In treatment 2a, anise scent was emitted into the colony from a single honeypot injected with 500 μL of sucrose solution scented with anise essential oil (333 μL·L^{-1}). Accordingly, the mode of learning could involve both olfaction and gustation since anise could be detected by both long-distance chemoreception (scent) and contact chemoreception (taste). In treatment 3, the scent was brought into the colony by successful 'demonstrator' foragers fed to repletion from an ad libitum gravity feeder, containing anise-scented sucrose solution, in a secondary foraging arena (Fig. 1). Here again, anise is a general chemosensory cue that can be detected by both scent and taste. In addition, the first two treatments (airborne and honeypot anise chemosensory cues) were also paired with artificial recruitment pheromone (treatments 1b and 2b), which evaporated from the same suspended glass vial (Table 1). Adding artificial pheromone was unnecessary for treatment 3 since successful foragers release natural recruitment pheromone when returning to the nest. The artificial recruitment pheromone used was a mixture of eucalyptol, farnesol and ocimene (at a concentration of 400 μL·L^{-1} acetone for each molecule: Molet et al. 2008), the three major bioactive components of the *B. terrestris* recruitment pheromone (Mena Granero et al. 2005). Each component was released in the nest at a rate of 0.24 μL h^{-1} by evaporation from the vial (i.e. similar to the application rate used by Mena Granero et al. 2005). We also conducted two controls where the suspended glass vial contained only

the solvent (acetone, treatment 4a) or the solvent and pheromone (treatment 4b). Controls (treatments 4a and 4b) were performed both before and after the experiments to ensure that treatment (1–3) effects had no long-term cumulative effect. Intervals between successive treatments or between the final treatment and the final control were typically 3–12 h and never exceeded 48 h. In order to restrict the potential treatment effects to modifying workers short-term preference for anise (over peppermint) and avoid changing their odour preferences in the longer term (e.g. Sandoz et al. 2000), we only exposed colonies to scent for short periods. Treatments were applied to the colonies only 10 min before starting tests of foraging preference. Moreover, the testing procedure always lasted less than 50 min, so colonies were not exposed to any treatment for more than 1 h.

In each experiment, motivated tagged foragers were tested individually in the foraging arena with an array of ten, unrewarded blue flowers, five of which were scented with anise and five with peppermint (Fig. 1). Scents were presented as aqueous solutions of 333 μL essential oil per litre of purified water (Essential Oils Direct, Oldham, UK), pipetted into the well of each flower. We recorded two types of behaviours: (1) approaches where the bee flies around a specific flower whilst being directly orientated towards it at a distance less than 3 cm and (2) landings where the bee lands on a flower. The test bee's foraging activity was recorded for 3 min after its first approach to a flower. Each forager was tested only once and was not allowed to return to the nest. Flowers were changed between tests to prevent bees using scent marks left by previously tested foragers as cues (Giurfa and Núñez 1992; Saleh et al. 2007). Controlled illumination for experiments was provided by high-frequency fluorescent lighting (TMS 24F lamps with 4.3 KHz ballasts, Philips, The Netherlands fitted with Activa daylight tubes, Osram, Germany) to simulate natural daylight with a frequency above the bee flicker fusion frequency.

Table 1 Colonies were exposed to seven different treatments

Treatment	Solution in suspended vial	Additional setup
(1a) Scent in air	Acetone+anise oil	–
(1b) Scent in air+pheromone	Acetone+anise oil+(eucalyptol, ocimene and farnesol)	–
(2a) Scent in honeypot	Acetone	Sucrose+anise oil in one pot
(2b) Scent in honeypot+pheromone	Acetone+(eucalyptol, ocimene and farnesol)	Sucrose+anise oil in one pot
(3) Scent brought back by forager	Acetone	Sucrose+anise oil in secondary arena+foragers
(4) Control	Acetone	–
(4b) Control+Pheromone	Acetone+(eucalyptol, ocimene and farnesol)	–

The scent (anise) was introduced to the nest either as an airborne cue using a suspended vial (treatment 1a), injected directly in the honeypots using scented sucrose solution (treatment 2a) or brought into the nest by demonstrator foragers allowed to feed on a scented sucrose solution (treatment 3). The effect of the recruitment pheromone was tested in the first two contexts (treatments 1b and 2b), but not with treatment 3 since successful demonstrator foragers release natural recruitment pheromone when they return to the nest. All chemicals were at a concentration of 333 μL·L^{-1} acetone. Controls assessed whether acetone (treatment 4a) or acetone and pheromone (treatment 4b) have any effect on scent learning

In total, we tested 136 bees, including 42 with airborne scent (treatments 1a and 1b), 37 with honeypot scent (treatments 2a and 2b), 15 with scent brought back by foragers (treatment 3) and 42 for control (4a and 4b). Among these 136 tests, 61 were with artificial pheromone and 75 without. We computed the percentage of anise-scented flowers approached by each bee (excluding approaches that led to landing). This measure of choice is continuous (0–100%) and is thus more informative than taking into account only the first approach behaviour (a binary choice). We also used the first landing event for each bee, as an alternative measure of scent choice. Continuous data (percentages of approaches) were analysed using analysis of variance (ANOVA), whereas binary data (first landings) were analysed using logistic regression. Percentage data were normally distributed so were not transformed. Because there was no colony effect, we pooled the data obtained from distinct colonies. All statistical analyses were performed using Statistica 7.1 (StatSoft, http://www. statsoft.com).

Results

On average, each of the 136 bumblebee foragers made 21.7 ± 1.8 (mean±SE) approaches to artificial flowers (excluding approaches that led to landing) and 2.1 ± 0.3 landings in 3 min. The percentage of bees whose first landing was on anise-scented flowers ranged from 21% to 93% ($N=96$ bees) with the lowest preference for anise over peppermint shown by bees in control groups (treatment 4) and the highest preference shown by bees exposed to anise scent brought back to the colony by a live demonstrator (treatment 3; Fig. 2a). Controls conducted before and after

application of treatments 1–3 all led to a low percentage of bees making their first landing on anise-scented flowers (<33%), indicating that these treatments had no long-term effect on foraging preferences.

Results of a logistic regression, excluding worker-collected scent (treatment 3) since it is always paired with the natural recruitment pheromone released by successful foragers, revealed a significant effect of how the anise chemosensory cue was introduced to the colony (Wald's $\chi_1^2 = 12.77$, $P<0.001$), but no effect of artificial pheromone on the bees' preference for a floral scent (Wald's $\chi_1^2 = 0.43$, $P=0.51$). These results indicate that a bee's preference for anise- over peppermint-scented flowers depends on how the bee encounters anise in the nest (i.e. no scent, airborne scent, or taste and scent from honeypots), but that the presence/absence of artificial pheromones paired with these scent cues are unimportant. Accordingly, we pooled pheromone and non-pheromone data (i.e. treatments 1a with 1b, 2a with 2b, and 4a with 4b), which allowed inclusion of data from worker-collected scent (treatment 3). The logistic regression performed on this complete dataset confirmed the significant effect of how the anise chemosensory cue was introduced (Wald's $\chi_1^2 = 19.42$, $P<0.001$). The percentage of landings on anise-scented flowers increased from control with colonies unexposed to any scent (28%), to anise scent provided in the air (43%), to anise-scented sucrose solution injected into a honeypot (75%) and finally to anise-scented sucrose brought back to the nest by demonstrator foragers (93%; Fig. 2a). This association between landing choice on anise-scented flowers and how scent is brought into the colony was significant (Pearson's $\chi_3^2 = 23.41$, $P<0.001$). We could not compare these data using pairwise chi-squared tests because power analyses indicated that such
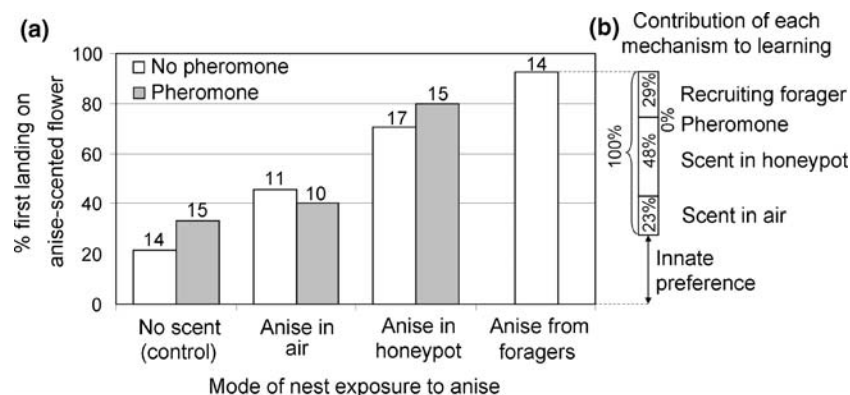
Fig. 2 First landing choice of foragers in response to how anise scent was brought into the colony and presence/absence of recruitment pheromone. **a** An increase can be observed from control to airborne scent, to direct injection in honeypot and to scent brought back to the nest by demonstrator foragers. The number of bees per treatment are given above each column. **b** Additive contributions (scaled to 100%) made by each scent-learning mechanism to worker choices of floral odour on which to forage when a successful forager performs recruitment. Scent and taste are important, as well as the presence of a recruiting forager. The recruitment pheromone does not appear to facilitate the learning process

tests would only have 8–50% chance of achieving statistical significance. Our results suggest that maximum learning performance, obtained when anise-scented sucrose is brought back to the nest by demonstrator foragers, i.e. the natural situation, can be broken down into several likely learning mechanisms. We present the percentage contribution of each mechanism in Fig. 2b.

We analysed the approach data using a two-way ANOVA (N=121), the two factors being: (1) the way the chemosensory cue was introduced in the colony (three levels: airborne scent, honeypot scent, control; worker-collected scent was excluded) and (2) the presence of artificial pheromone (two levels: with or without pheromone). This revealed no significant effect of either the way the chemosensory cue was introduced in the colony ($F_{2,115}$=0.18, P=0.84) or presence of artificial pheromone ($F_{1,115}$=0.58, P=0.45). The interaction between these two factors was also non-significant ($F_{2,115}$=0.92, P=0.40). In all treatment combinations, there were no significant differences in the percentage of anise-scented flowers approached by foragers (post hoc pairwise t tests with Bonferroni correction: adjusted α=0.0056, smallest P=0.17, common mean for the approach of anise-scented flowers=53.4±1.2%). Accordingly, we pooled pheromone and non-pheromone data and we included the data from worker-collected scent. The percentage of approaches to anise-scented flowers was lowest (52.9±2.1%) for the control, i.e. when the colony had not been exposed to any scent. The choice percentage was similar when anise scent was provided in the air, a fraction higher when anise scent was provided in a honeypot (+3% relative to control) and a little higher when anise scent was collected and brought back to the nest by demonstrator foragers (+12% relative to control). Overall, there was no significant effect of how anise chemosensory cue was introduced to the colony (one-way ANOVA N=136: $F_{3,132}$=0.98, P=0.40; Fig. 3). Post hoc tests indicated that differences were not significant (pairwise t tests with Bonferroni correction for multiple comparisons: adjusted α=0.0083, smallest P=0.11). Moreover, the number of approaches performed before the first landing did not depend on how the anise chemosensory cue was introduced to the colony ($F_{3,90}$=0.55, P=0.65).

Discussion

Our results show that bumblebee workers can learn a floral odour brought into the nest in different ways. We have identified factors responsible for 71% of the learning of floral scent, i.e. olfaction of airborne anise scent and contact chemoreception (taste) of anise in nectar (Fig. 2b). The remaining 29% is linked to the presence of a recruiting forager inside the nest. Several phenomena could be
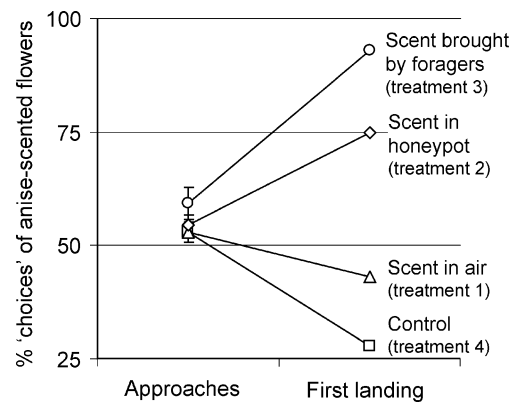
Fig. 3 Preference for anise (over peppermint)-scented flowers as determined by approach and first landing choices. *Left* mean (±SE) percentage of approaches of anise-scented flowers made by bees in each treatment (sample sizes given in the "Materials and methods" section). *Right* percentage of bees whose first landing behaviour was on an anise-scented flower in each treatment group (sample sizes given in Fig. 2). There was no significant effect of how anise chemosensory cue was introduced to the colony on the percentage of approaches to anise-scented flowers. In contrast, choice data based on first landing show distinct differences among treatments. *Lines* linking approach and first landing data for each treatment do not cross, indicating that irrespective of the selected measure of choice, treatment order remained the same. Pheromone and non-pheromone treatments were pooled since there was no significant effect of pheromone

involved, as discussed later, and further investigation is thus required. However, our results demonstrate that the presence of recruitment pheromone does not facilitate the process of scent learning.

Learning is based on olfaction and gustation

The presence of an odour in the ambient air within the bumblebee nest is itself sufficient for scent learning, even if the exposure time is short (only 10 min for the first bee tested during each experiment). Similarly, in honeybees, the presence of an unrewarded scent in the nest over several days is sufficient to promote preferential orientation towards that scent in an olfactometer. However, such learning is clearly not appetitive since honeybees that have been exposed to the scent show lower learning performance during proboscis extension response (PER) conditioning assays (Pham-Delègue et al. 1990; Jakobsen et al. 1995; Sandoz et al. 2000). Accordingly, long-term exposure to scent seems to cause familiarisation, i.e. the scent is considered as part of the colony odour, hence preferential orientation. In contrast, when honeybee foragers provide scented nectar to their nestmates by trophallaxis during recruitment, the acquired memory can be retrieved in the PER paradigm, indicating that appetitive learning has occurred (Farina et al. 2005). Differences in learning can be expected depending on whether exposure to a scent

inside a honeybee or bumblebee nest was long or short. Long exposures seem to cause familiarisation, whilst short exposures to a new scent may trigger appetitive learning. This still has to be tested in both honeybees and bumblebees using the PER.

Scent-learning performance inside the bumblebee nest improves if the odour is present in the nectar stored in honeypots (compared to when it is only present as an airborne scent). This could be explained in a number of ways: firstly, when the odour occurs together with a sucrose reward, an association can be formed because imbibing the nectar from the honeypot is paired with the scent. In contrast, when odour cues are only present in the air inside the colony, the scent is only directly paired with sucrose rewards if the forager is feeding from honeypots (probably only a small fraction of the time during which the bee is exposed to the airborne scent). Secondly, offering anise in sucrose may involve an additional sensory modality, gustation, in addition to olfaction (De Brito Sanchez et al. 2007) and thus improve learning by activating two sensory pathways. There is considerable overlap between olfactory and gustatory receptors in *Drosophila* (Robertson et al. 2003), and this may also be the case in bumblebees. Accordingly, similar molecules could be detected by distinct olfactory and gustatory receptors. Finally, scent may be more intense when released from scented sucrose in a honeypot than from a suspended vial. It is difficult to know which mechanism is the most influential. When a honeypot was injected with scented nectar, it was rapidly emptied by a group of bees, consisting mainly of non-foragers, probably to be processed into honey. The extent to which each tested bee was in contact with that nectar is unknown. In honeybees, learning a floral odour can occur during direct food transfer between nestmates by trophallaxis (e.g. Grüter et al. 2006). However, bumblebees do not perform trophallaxis, so associative learning must involve direct contact with nectar in honeypots.

Learning is improved by the presence of a recruiting forager

Because nectar from different sources and scents are present in the nest, workers must be able to recognise and learn new scents, so that they forage on flowers that are currently rewarding instead of looking for flowers that provided the nectar stored in the nest. It is possible that bumblebees can discriminate freshly added nectar from older stored nectar since the latter contains glandular secretions after being processed by workers (Dornhaus and Chittka 2004). If so, workers could preferentially search for flowers that smell like the fresh nectar found in the nest. An alternative solution would be for bees to learn scents associated with the presence of recent successful foragers, i.e. those which have recently returned to the nest, secreting foraging recruitment pheromone. Indeed, we found that the presence of such foragers further improves odour learning. However, it appears that the recruitment pheromone itself does not facilitate this learning process. There are a number of alternative mechanisms by which the presence of active successful foragers could facilitate scent learning. Foragers could leave short-lived glandular secretions in the regurgitated nectar. Moreover, freshly regurgitated nectar is likely to be warmer than stored honey, making it more attractive to nestmates. Finally, during excited recruitment runs, foragers create air movement by wing fanning, they produce sound and substrate vibration and they bump into and climb over other workers (Dornhaus and Chittka 1999). All these factors may play an important role in nestmates learning new floral odours, and should thus be assessed in future research.

Approaches are exploratory behaviours

We found that approaches to flowers were much less informative than landings when considering treatment differences in choice behaviour (Fig. 3), even though we collected ten times more approach than landing data. Furthermore, treatments did not influence the number of approaches made before a bee made its first landing. Making flower choices appears to be a hierarchical procedure. Bees first approach a flower to inspect its scent, if it passes inspection they will typically land and finally they will probe the flower to assess the nectar it contains. Approach flights in nature are largely visually guided, so flowers can be rejected from a distance. In contrast, our experiments involved visually identical flowers, so only a closer inspection (within 3 cm of the target flower) allowed our bees to assess floral type based on scent. Approaches appear to be exploratory behaviours, so it is unsurprising that approach data are much less informative than landing data when comparing treatments. Accordingly, such data should be used with caution and combined with the recording of landing or feeding that appear to more accurately reflect real choices.

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