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Food alert in bumblebees (*Bombus terrestris*): possible mechanisms and evolutionary implications

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Abstract The return of a successful bumblebee forager stimulates nestmates to leave the nest and search for food. Here we investigate the mechanisms by which this happens. Successful *Bombus terrestris* foragers perform irregular runs in their nest, often lasting for several minutes. Run duration is at its maximum when food has just been discovered. Running likely serves to distribute a pheromone, since the information flow between “runners” and “recruits” can be disrupted by eliminating air exchange, while leaving other potential means of communication intact. In addition, nectar stores in the nest may be monitored continuously. A sudden influx of nectar into the nest also causes measurable increases in forager activity. The implications of bumblebee recruitment behavior for the evolution of communication in bees are discussed.

Keywords Communication · Pheromone · Foraging · Bee dance · Recruitment

Introduction

Communication about food sources is common in social insects and enables colonies to coordinate and regulate their foraging activity according to food availability and demand (Seeley et al. 1991; Seeley and Tovey 1994). Such communication can take place either at the food source itself or at the nest, where a forager can potentially interact with all other individuals of the colony. In eusocial bees – the honeybees, stingless bees, and bumblebees – diverse communication systems have evolved, differing both in information transmitted and in mechanisms. In some species, such as bumblebees (*Bombus terrestris*; Dornhaus and Chittka 1999) and some species of sting-

less bees, for example *Trigona angustula*, *T. iridipennis*; (Lindauer and Kerr 1960; Esch et al. 1965; Kerr 1969), communication merely involves an alerting signal, which conveys that food is available. In other species, for example the stingless bee *Scaptotrigona postica*, information about profitable foraging sites is communicated by laying scent trails to them (Lindauer and Kerr 1960). In some other species of stingless bees, such as *Melipona panamica* (Nieh and Roubik 1995) and all species of honeybees (Lindauer 1956; von Frisch 1967), recruitment systems are sophisticated and enable foragers to communicate the precise location of profitable food sources (von Frisch 1967). These more advanced systems of information exchange make use of repetitive motor patterns, sounds, and substrate vibrations (Esch et al. 1965; von Frisch 1967; Kirchner and Dreller 1993; Tautz 1996; Nieh 1998).

Bumblebees mark food sources with odors (Cameron 1981; Stout et al. 1998), but leave no scent trails unless they walk (Chittka et al. 1999), which means foragers can obtain information on the quality of food sources through pheromone signals in the field. At the nest, bumblebees also receive information on food availability and floral odor (Dornhaus and Chittka 1999). If one bee forages successfully, other bumblebees in the nest are induced search for food sources, preferably with the same odor as the food collected by the successful bee. The mechanism by which this happens has not yet been investigated. Here we present evidence that recruits obtain information on foraging conditions using at least two sources of information. The colony's nectar stores function as a cue by which bees can find out whether successful foraging is taking place. In addition, bees are induced to start foraging through a pheromone signal which is probably distributed by the successful foragers.

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Methods

General setup

The experiments were conducted with laboratory colonies of *B. terrestris*. They contained a queen and 50–150 workers. The

nest was contained in a wooden box (15×13×10 cm), which was connected to a foraging arena (50×70×30 cm) with a transparent plexiglas tube (15 cm). The bees were fed by placing a feeding dish filled with 1:1 (v/v) sucrose/water solution in the arena. For individual recognition, bumblebees were marked with numbered plastic tags glued to the thorax.

Forager behavior

To examine behavior of forager bees and thus the means by which successful foragers induce other bees to search for food, we allowed only a single worker into a foraging arena which contained a sucrose feeder. That bee was allowed to conduct six consecutive foraging trips. No other bees were allowed to collect food during this time. On different days, a total of 114 active foragers of 15 colonies were tested in this fashion. We quantified the duration of in-nest stays of foragers as a possible time investment in communication, and for 33 foragers, the time spent before and after unloading. Seven foragers were videotaped during the entire time in the nest on all six trips, and their behavior analyzed regarding number and length of fanning bouts, contacts with other bees, and occurrence of grooming behavior. The number of honeypots probed by the forager before and after unloading was counted.

To test if the forager might influence nestmates, we analyzed nestmate behavior, including their movement speed. We videotaped the bees' behavior in the nest when no food was being collected (resting colony) and after 30 min of food collection by a single forager (alerted colony). In both cases, no bees except the single forager were allowed to leave the nest. Path and movement speeds of bees were analyzed using frame-by-frame video analysis. Thirteen randomly picked bees were observed for 7 s each in the resting colony and 30 bees for 17 s in the alerted colony.

Possible signals

We were interested in whether a forager's motor behavior (and the food she brings home) are necessary to alert nestmates, or whether other signals, such as substrate vibrations or pheromones might be essential. To this end, we used a setup in which direct contact between foragers and potential recruits was made impossible. The nest boxes of two colonies were placed beside one another. Each had a window of 5×5 cm in one side, covered with wire mesh. These windows faced each other so that the wire meshes were approximately 1 cm apart. Each nest box was connected to its own foraging arena to which bees had free access. One colony was designated the "test colony", the other was the "foraging colony". We tested whether successfully foraging bees in the latter had an effect on the activity of the test colony. Our measure for the number of bumblebees motivated to forage was the number of bees leaving the nest per unit time, in the following termed "activity level." This was measured by constantly counting the number of bees moving outward past a marked point in the tube leading to the foraging arena. The test colony's activity level was monitored continuously.

Nine trials with the same two colonies were conducted, each consisting of a 30-min control phase and, immediately after this, a 60-min experimental phase. During control phases, none of the colonies had access to food. During experimental phases, a feeding dish was placed in the arena of the "foraging colony". Foragers from this colony could then collect food, and if they produced signals transmittable through a wire mesh, the test colony was expected to react by increased activity as well. To further investigate the modality of the potential signal, the experiment was repeated in another ten trials with the same colonies as before, with a thin sheet of transparent plastic wrap inserted between the wire meshes of the two nest boxes. The light transmission properties of the plastic wrap were uniform across wavelengths visible for bees (including UV light). The plastic wrap prevented circulation of odors between the two nests. Signals of other modalities – airborne and substrate vibrations and visual cues – should not have been sub-

stantially impaired compared to the condition without the plastic wrap.

Nectar stores

Nest bee reaction to successful foraging by other bees need not necessarily be related to signals emitted by these foragers. We tested the hypothesis that increased foraging motivation is elicited by an influx of nectar to the colony's food stores alone. The activity level of the colony was measured as above. On test days, colonies were not fed but had free access to the arena in which food was usually presented. We conducted 14 test runs, each with control and experimental phases. Each test run consisted of a 30-min control phase and a 60-min experimental phase. During both of these, the colony's activity level was measured; since a colony's activity level takes approximately half an hour to increase, only the activity level during the second half of the experimental phase was compared to the activity level during the control phase. In the experimental phase, 100 µl of sucrose solution was injected with a pipette into one of the nest's honeypots every 5 min. This is equivalent to the amount and frequency of nectar collection by a bee in this foraging arena setup (Dornhaus and Chittka 1999).

To control for possible disturbance effects of inserting a pipette into the nest every 5 min, we conducted ten control runs, during which a pipette was inserted into the nest every 5 min but no sucrose solution was injected.

Results

Forager behavior

Successful bumblebee foragers often spend many minutes in the nest before exiting again for a new foraging trip. These foragers perform "excited" runs on the nest structure (Fig. 1), bumping into and climbing over other workers, from time to time fanning their wings. Their movements are entirely irregular: there are no repetitive paths. There is no obvious coding of information about food location in these movements, unlike the stereotyped motor patterns ("dances") of honeybees. During these activities, bumblebee foragers will sometimes probe a few honeypots and unload their forage into one of them. The median number of honeypots probed was 1 [interquartile range (IQR)=6] before unloading (excluding the pot used for unloading) and 0 (IQR=1) afterwards (Wilcoxon test, $P=0.001$, $n=40$). The number of pots probed correlated with the time spent in the nest ($P<0.0001$, Spearman's rank $R=0.65$), and most probing took place on the first trip [median 11 honeypots (IQR=7) compared to a median of 1 (IQR=1) on the sixth trip; Wilcoxon test, $P=0.046$, $n=6$]. Probing might serve to find a suitable pot for unloading, but could also function to survey nectar stores. After unloading, a bee might spend several more minutes running around before leaving for another trip to the food source. We measured a maximum of 10 min of excited running before the forager exited again, whereas the minimum time measured for unloading and leaving the nest was only 13 s. The average (\pm SE) time spent in the nest was 105 ± 5.4 s, with large differences between individuals (Fig. 2). The time spent running in the nest between foraging bouts depended on how many bouts had already been completed

Fig. 1 Path of a forager in the nest box during an in-nest stay of 5 min (black line) and of a non-forager in the same time interval (gray line). The black frame indicates the size of the nest box. The nest itself covers most of this area, honeypots and brood cells being scattered across its surface. The entrance to the box is in the middle of the wall to the right

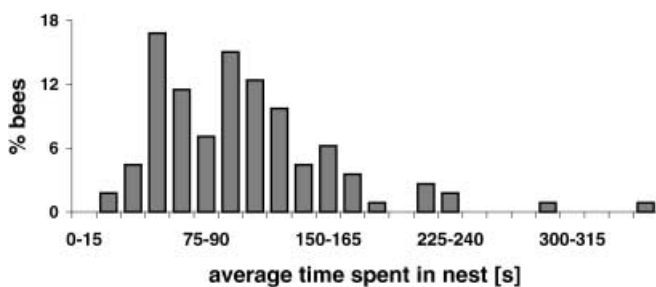
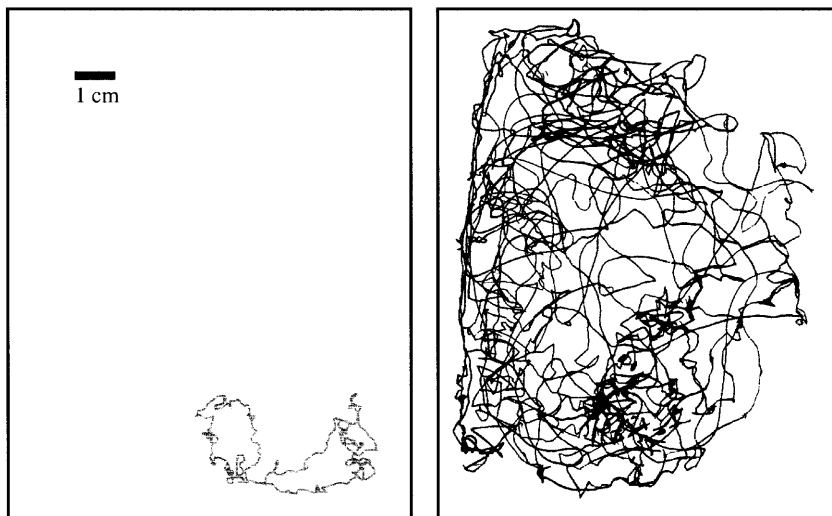


Fig. 2 Frequency distribution of average time each bee spent in the nest ($n=114$ bees)

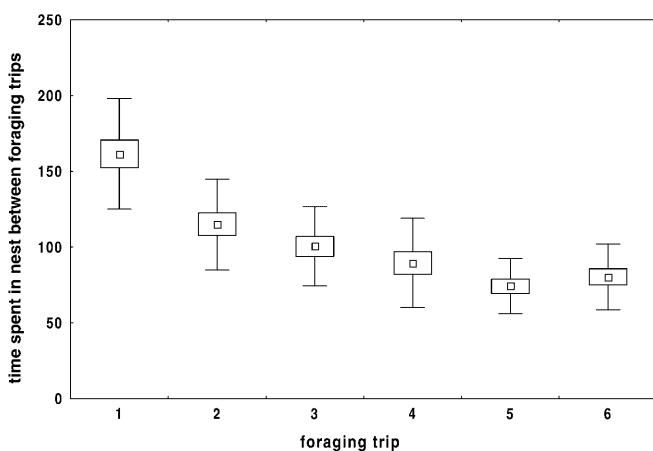


Fig. 3 Duration of in-nest stays of foragers depends on the number of foraging trips completed (shown are the average, SE, range without extremes: distance from average $>4 \times SE$)

(Fig. 3). For the first trip after the food source had been discovered, the average time a forager spent in the nest was 162 ± 9.1 s, while on the sixth trip of the same foragers, it was only 80 ± 5.4 s [paired t -test, $P < 0.00001$, $n=104$; data were normally distributed with $P < 0.01$ (Lilliefors test)]. Bees spent significantly more time in the nest after than before unloading [median time 15 s

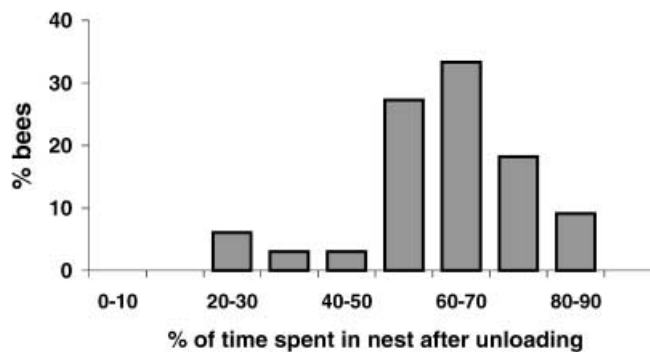


Fig. 4 Frequency distribution of time spent in the nest after unloading ($n=33$ bees)

(IQR=23 s) before versus 35 s (IQR=19 s) after unloading; Wilcoxon test, $P < 0.001$, $n=33$ bees]. The relationship did not change with trip number (Wilcoxon test, $P=0.82$, $n=32$) but varied between bees (Fig. 4). The fact that foragers spent more time in the nest after than before unloading, while probing into pots took place before, indicates that these runs serve a function independent of nectar deposition or surveying of stores. The behavior of foragers was analyzed in more detail to investigate whether the runs in the nest could be an investment in communication.

The bees could often be seen fanning their wings while running around in the nest between their foraging trips. Median lengths of these fanning bouts was 0.89 s (IQR=0.71, $n=35$) and the median number of bouts per in-nest stay was 4.5 (IQR=7.5, $n=42$). Most of this fanning took place after unloading: median fanning duration per time spent in nest was 0.0% (IQR=8.7%) before and 7.5% (IQR=12.7%) after unloading (Wilcoxon test, $P=0.021$, $n=38$). The fanning duration per time in nest also declined with trip number (Wilcoxon test, $P=0.028$ for a comparison of the 1st and 6th trip, $n=6$; Fig. 5). Fanning behavior thus occurs when the forager spends more time in the nest.

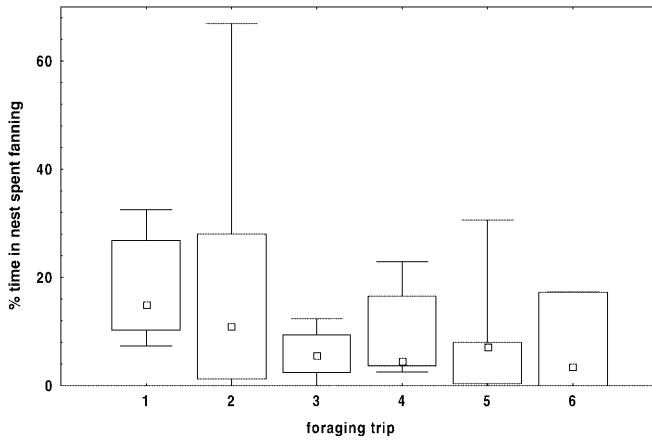


Fig. 5 Duration of fanning, as percentage of time spent in the nest, is dependent on the number of foraging trips completed (shown are the median, interquartile range, and range)

In 91% of bouts, bees groomed themselves when in the nest, i.e., legs were used to stroke over body parts (head in 29%, thorax in 8%, abdomen in 36%, wings in 23% of grooming instances). Grooming always took place after unloading (in a total of 42 filmed trips we never observed grooming before unloading). The function of grooming might be to remove wax accidentally picked up while bees probe honeypots, or to distribute a pheromone over the body (see below).

We never observed extended interactions of the forager bee with other bees of the colony. Most contacts appeared to be accidental quick touching or pushing by the forager forcing her way around on the nest. Other bees did not show immediate reactions to contacts. The median number of such contacts per time in the nest was 0.89/s (IQR=0.30/s), and did not change after unloading (Wilcoxon test, $P=0.77$, $n=35$). It declined slightly with trip number, from a median of 1.04/s on the first to 0.86/s on the sixth trip (U -test; $P=0.015$ for a comparison of the first and second with the fifth and sixth trips, $n=13$). Because there seemed to be no deliberate tactile interactions between the forager and other bees, we suppose that no signal dependent on physical contact is involved in alertment behavior.

Bees in the nest never attempted to follow the running bee, but while she pumped her foraging load into a honeypot, several other bees often gathered around that bee and probed the new nectar immediately after the forager removed her head. Some of these bees immediately displayed increased levels of motor activity and headed toward the hive exit. After a forager had collected food for half an hour (equaling approximately six round trips to and from the food), other bees in the nest moved faster, even though they had not had contact with the food source themselves and this conditions outside the nest had not changed in this time period; this movement created the impression of “excitement” in the hive. The median speed of bees in the nest of a colony without an active forager (resting colony) was 0.40 cm/s ($n=13$), whereas the median

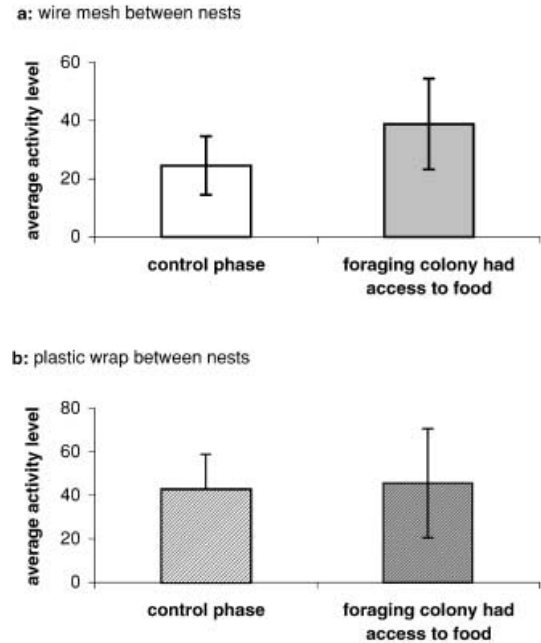


Fig. 6a,b Comparison of the average activity levels of the test colony during the control phases and the second half hour in which the foraging colony was fed

speed of bees in the nest after one bee had been foraging for 30 min (alerted colony) was 1.18 cm/s (Mann-Whitney U -test, $P<0.00001$, $n=30$). The forager’s speed when in the nest after half an hour of foraging was 2.83 cm/s.

Possible signals

Active foragers had a positive influence on the foraging activity of other bees, even if direct contact between them did not take place. The activity level of the test colony, without access to food inside or outside the nest, increased significantly when the colony next to it was foraging (Fig. 6a; Wilcoxon test, $P<0.05$, $n=9$). Information that food was available must have been transmitted through the wire mesh. In contrast, the activity level of the test colony did not increase significantly when the other colony was foraging if the two colonies were separated by a sheet of plastic wrap (Fig. 6b; Wilcoxon test, $P=0.58$, $n=10$). The stimulus that generated the effect in the previous experiment must have been impaired by the plastic wrap, while being transmissible through a mesh. This points to a stimulus dependent on the exchange of air between the two nests, which would be the case for a pheromone. Stimuli of other modalities, such as visual or mechanical signals, would not have been inhibited by the plastic wrap any more than by the wire meshes separating the two colonies.

Nectar stores

By manipulating nectar stores, a higher activity level could be induced in the bumblebee colonies. The activity

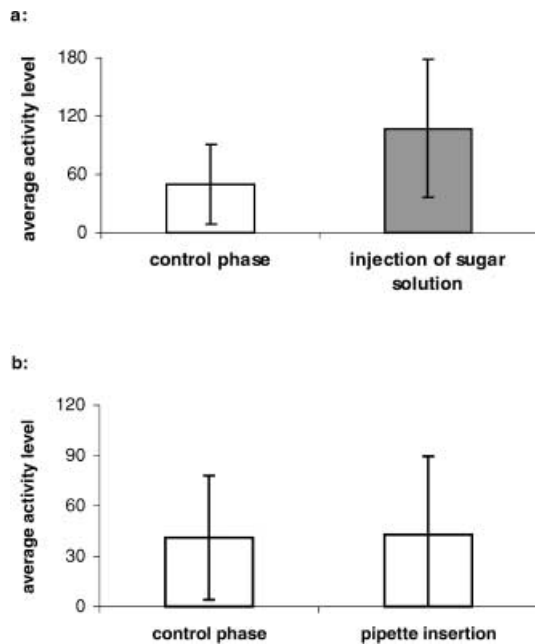


Fig. 7a,b Activity levels during the half hour before (control phase) and the second half hour after injection of sucrose solution into the nest's honeypots

levels during periods in which sucrose solution was added to the colony's nectar stores were significantly higher than during control phases (Fig. 7a; Wilcoxon test, $P < 0.01$, $n = 14$). Inserting a pipette into the nest without injecting sucrose solution had no significant effect on activity levels (Fig. 7b; Wilcoxon test, $P = 0.96$, $n = 10$). The increased activity seen in the nectar injection experiment was thus not due to an alarm reaction caused by the insertion of the pipette into the nest, but to the influx of sugar solution.

Discussion

In *B. terrestris*, foraging activity at the colony level is adjusted via the activity of successful foragers and changes in the nectar stores. The extensive movements of the active foragers likely cause at least some of the effect, but conclusive evidence for this hypothesis is difficult to obtain: mimicking the movements of a bumblebee forager running across the nest, while eliminating other signals that it might emit during its runs within the nest is not easy. Foragers spent substantially more time in the nest between foraging trips than is needed to find a suitable honeypot. In fact, they spent more time in the nest *after* they had unloaded, and often groomed and fanned their wings after unloading. Fanning, grooming and fast running might directly or indirectly serve a communicative function. Our two-nest experiments provide conclusive evidence that recruits are activated even when direct mechanical contact between foragers and recruits is eliminated. Even though returning bumblebee foragers sometimes buzz their wings in characteristic short pulses

(Heidelbach et al. 1998), the mode of information transmission is unlikely to be airborne sound: such sounds are heard by bees only over an extremely short range (Tautz 1979; Michelsen et al. 1987) and thus would not be perceived by bees through our double wire mesh setup. The bees in the test colony might have visually gauged the high motor activity in the neighboring nest. Natural nests of *B. terrestris* are, however, subterranean, so that within-nest activities take place in almost complete darkness. Thus, visual cues are unlikely to play any role in natural nests. Moreover, even though bees were allowed visual contact in the two-nest experiment, information was not transmitted unless air exchange took place.

Foragers might also employ substrate vibrations to recruit other bees, as in honeybees and stingless bees (Esch et al. 1965; Tautz 1996). Again, we consider this an unlikely explanation for signal transmission in our bees, since a plastic wrap would not impair substrate vibrations. Thus, it seems most likely that a chemical signal, probably a volatile pheromone, is released while foragers run around the nest, and running and fanning might serve to distribute such a pheromone efficiently. It triggers increased motor activity in the nest and causes more bees to start foraging. Further research must identify the chemical nature of this pheromone, and the glands that produce it. This will be interesting not only from a physiological and comparative point of view, but also from an applied perspective, for example the control of the activity of bumblebees used to pollinate crops in greenhouses.

The running activity of successful foragers declines with the number of completed foraging bouts. This coincides with increased foraging activity of recruits, which clearly makes sense: once the forager force of a colony has been activated, time need no longer be devoted to recruitment. The feedback mechanism causing foragers to spend less time recruiting has not yet been identified. Foragers might assess the activity of other bees, count their own foraging bouts, or respond to increasing nectar stores. These stores are, apparently, also monitored by inactive foragers, for when nectar was experimentally added to a colony's honeypots, its foragers reacted by leaving the nest to search for food. Whether bees sense the new nectar by its concentration (nectar has a lower sugar concentration than honey; Heinrich 1979), or whether bees memorize, and continuously check, the level in the colony's honeypots is not known.

Before departing on a foraging trip, a bee can obtain information on general food availability as well as on the scents of profitable flower species (Dornhaus and Chittka 1999). No information about food location is available. Bumblebees of several subgenera and from temperate to tropical habitats [*B. (s. str.) terrestris*; *B. (Megabombus) agrorum* (now *pasuorum*), *B. (Pyrobombus) hypnorum*, and *B. (Fervidobombus) atratus*] have been shown not to recruit nestmates to particular places (Jacobs-Jessen 1959; Esch 1967; Kerr 1969; Dornhaus and Chittka 1999). Jacobs-Jessen had already noted the extended, but irregular runs of returning for-

agers in the first three of the above species. Such behavior was also observed in *B. (Pyrobombus) impatiens* and *B. (s. str.) occidentalis* (Chittka and Dornhaus 1999). None of these studies tested for an alerting effect. Controlled experiments, along the lines of those of Dornhaus and Chittka (1999), are needed for more species of bumblebee to confirm that the behavior patterns observed here for *B. terrestris* are generally valid among the bumblebees.

What do bumblebees tell us about the evolution of recruitment in the social bees? Can we deduce from bumblebee behavior, the origins of one of the most intriguing systems of animal communication, the honeybee waggle dance? This question requires a comparison of the honeybee recruitment system with those of their close relatives, the stingless bees and bumblebees (which are presumed to be sister groups; Cameron 1993). Bumblebees share with stingless bees the highly irregular (possibly excitatory) runs within the nest between foraging bouts (Lindauer and Kerr 1960; Kerr 1969; Nieh 1998). These runs lack any obviously repetitive patterns, as opposed to the figure-eight-shaped waggle dance of the honeybees. Therefore, we might conclude that the common ancestor of the social bees possessed irregular runs which predated the more sophisticated, location-coding, dances of honeybees, assuming that the last common ancestor of honeybees and bumblebees was social. There are two caveats, however. First, there is a strong possibility of convergence: "excited" motor behaviors by successful foragers are known not only from social bees. In many species of ants, "fast runs" as well as waggle motor displays are part of recruitment behaviors (Hölldobler and Wilson 1990). Similarly, rapid running by foragers on the nest has been observed in some wasp species and has been suggested to have the function of stimulating nestmates (Richter 2000). The presence of this kind of behavior in groups that have evolved sociality independently of bees suggests that the occurrence of excited movements of foragers in the various groups of social bees might be a result of convergent evolution rather than common ancestry (homology). The common ancestor of the stingless bees and bumblebees might have possessed an excitatory motor display but, unfortunately, the motor activities of stingless bees and bumblebees are too irregular to be behavioral traits whose homology is unambiguous (such as the movements coding distance and direction in the waggle dances of the various species of honeybee; Dyer 1991).

There is a second argument that suggests independent origins of the honeybee dances and the irregular runs of the bumblebees and stingless bees. Honeybees do have a recruitment behavior with similar information content as the runs of bumblebees, but the behavior displayed by honeybees is wholly unlike that of bumblebees. In their "round dances," honeybees run in circles, alternating between a clockwise and anti-clockwise direction, frequently wagging their abdomen. This behavior serves to alert nestmates to nearby food sources, informing them about the odor of the food via floral scent carried on the

dancer's body surface, but not informing them about the location of food sources (von Frisch 1967). Thus, the information transmitted is the same as in bumblebees, but the path of the honeybees' round dance is highly regular. There is no conceivable selection pressure for honeybees to evolve a round dance if their ancestors already had behavioral means which, albeit seemingly more primitive, conveyed the same information. Thus, the honeybee waggle dance is more likely to have evolved from ritualized intention movements (aborted flights toward the target), as suggested by Haldane and Spurway (1954) and von Frisch (1967), rather than from irregular excitatory movements of successful foragers via the round dance. The round dance is evidently a high-speed derivative of the waggle dance, used to indicate the presence of nearby food (Kirchner and Lindauer 1988; Jensen and Michelsen 1997).

For evolutionary arguments, it would also be useful to know if the extended running behavior of bumblebee foragers has any excitatory function in itself, or if it simply serves to distribute a pheromone with low volatility around the nest. If that is the case, are bumblebees unique in terms of pheromone recruitment? Or do other social bees have similar pheromones? Honeybee dancers have been suggested to use a pheromone to attract other bees in the hive (Tautz and Rohrseitz 1998), but direct evidence for this proposal is lacking. It is common beekeeper knowledge that honeybees (like bumblebees) can be stimulated to start foraging by injecting sugar solution into the hive. To our knowledge, information about similar phenomena in stingless bees is not available, and we do not know the mechanisms involved, which would be necessary to deduce homology. In conclusion, much information still needs to be collected to understand the early evolution of bee recruitment, and the ecological circumstances that produced its many variants. Bumblebees remain a key group in solving these riddles.

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