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Bumble bees (*Bombus terrestris*) store both food and information in honeypots

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Social insect foragers often transmit information about food sources to nest mates. In bumble bees (*Bombus terrestris*), for example, successful foragers use excited motor displays and a pheromone as communication signals. In addition, bees could make use of an indirect pathway of information flow, via the honey stores. We show here that, indeed, bees in the nest continuously monitor honeypots and sample their contents, thus obtaining information on supply and demand of nectar. When there is an influx of nectar into the nest, the colony deploys more workers for foraging. The number of new foragers depends on sugar concentration. Foragers returning with high-quality sugar solution display more "excited runs" on the nest structure. The recruits' response, however, does not depend on modulated behavior by foragers: more workers start to forage with high quality of incoming nectar, even when this nectar is brought by a pipette. Moreover, we show that the readiness of bees to respond to recruitment signals or incoming nectar also depends on colony demand. When colony nectar stores are full, the response of bees to equal amounts of nectar influx is smaller than when stores are empty. When colony nectar stores are depleted, foragers spend more time running excitedly and less time probing pots in the nest and run with higher average speed, possibly to disperse the alerting pheromone more efficiently. However, more bees respond to nectar influx to empty stores, whether or not this is accompanied by forager signals. Thus, honeypots serve to store information as well as food. *Key words:* collective behavior, communication, foraging, information flow, recruitment, social insect. *[Behav Ecol 16:661–666 (2005)]*

Social insect colonies have been termed superorganisms because in many respects they resemble organisms rather than collections of independent individuals (Seeley, 1989; Wheeler, 1911). For example, they exhibit complex behaviors that require extraordinary coordination between group members. Examples of such collective behaviors are the selection of a favorable new nest site among alternatives (Mallon et al., 2001), allocation of foragers to the most profitable food patches (Seeley et al., 1991), and regulation of the number of workers engaged in a task according to the colony's needs (Beshers and Fewell, 2001; Hölldobler and Wilson, 1990; Seeley, 1995). These behaviors are not the result of the management of the colony by a single "brain" or leader but emerge from the actions of many individuals. Each of these individuals only has access to limited information about the system as a whole.

To coordinate their actions, individuals exchange information. Social insects are known for the multitude of different communication signals they can produce, using several different modalities (Hölldobler, 1999; Hölldobler and Wilson, 1990; Seeley, 1995). Signals can be directed at specific individuals or at whole groups (Hölldobler and Wilson, 1990), and they have evolved for the purpose of information transmission. There are also, however, other pathways of information flow, which are called "cues" as opposed to "signals" (Seeley, 1998). When individuals pick up information from the behavior of other individuals, and that behavior has not evolved for the purpose of transmitting information, they are using cues (Brown, 1988; Danchin et al., 2004; Seeley, 1998). Cues cannot only be extracted directly from another individual's behavior. We show here that honeypots in the bumble bee species *Bombus terrestris* provide information as a by-product of the foraging process. By monitoring the honeypots, bees collect information about both the supply of food outside the nest and the demand for food inside the nest.

Foraging in bees is an activity that can be both risky and energy demanding (Goulson, 2003; Heinrich, 1979; Seeley, 1985). A bee colony should thus regulate the number of bees searching for food depending on the expected costs and benefits, which will depend in part on current foraging conditions and the colony's demand for food. Such regulation of foraging activity is achieved through information exchange between active foragers and other bees in the nest. In the bumble bee *B. terrestris*, information on the favorability of nectar foraging is available to bees in the nest through two channels. First, bees monitor honeypots for an influx of nectar, which is an indicator of successful foraging by other bees (Dornhaus and Chittka, 2001). Second, when a forager has discovered a good food source, she performs "excited runs" on the nest (Dornhaus and Chittka, 2001), distributing a pheromone signal (Dornhaus et al., 2003). In response to nectar influx or such pheromone signals, previously inactive bees start to search for food. Foraging activity is thus adjusted to the presence of food sources (Dornhaus and Chittka, 2004).

Foraging activity might also be adjusted to demand in these bumble bees. In contrast to honey bees, bumble bee colonies usually only contain honey stores sufficient for a few days (Heinrich, 1979). This indicates that possibly there is a down-regulation of foraging activity when enough nectar has been collected because without such regulation bumble bees could accumulate much larger amounts when foraging conditions are good.

Here, we test whether information on the quality of available food sources is transmitted between active and potential bumble bee foragers in the nest. We investigate

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whether bees can extract such information from honeypots or whether foragers might communicate it directly. In addition, we test whether the colony's current food demand in the nest influences forager behavior or the bumble bees' responsiveness to information about new food sources.

MATERIALS AND METHODS

In all experiments, queenright laboratory-reared *B. terrestris* colonies (obtained from Bunting Brinkman Bees, Belgium, and Koppert Biological Systems, Netherlands) were used. The colonies contained between 25 and approximately 200 workers. They were housed in wooden nest-boxes (26 × 14 × 10 cm), each of which was connected to two foraging arenas (40 × 60 × 30 cm) with a Y-shaped, transparent Plexiglas tube. Access to each arena could be controlled by the experimenter, using shutters inserted into slits in the tubes. The bumble bees had access to one of the foraging arenas at all times, but on experimental days there was no food provided in this arena. To investigate information transfer between an active forager and other bees, we supplied only one individual forager with information about the food source by allowing only a forager bee marked with a numbered plastic tag ("Opalithplättchen") access to the second arena, which contained food (experiments 1a and b, 2a and b). To investigate information flow through nectar stores, we manipulated honeypot contents, without any food source available to the bees in either arena (experiments 1c and 2c).

Nest-box and foraging arenas had transparent Plexiglas covers, so that the bees' behavior could be observed. On days when the bees were not used in an experiment, they were fed by placing a dish with 0.5 M sucrose solution (feeder) into the accessible arena. All sucrose solutions used in this study were unscented. Pollen was given directly into the nest-box. Bees were not fed sucrose solution on experimental days except as detailed in experiments.

Unless noted otherwise, a colony's response to a manipulation is quantified by measuring changes in the activity of that colony. The activity is defined as the number of bees leaving the nest per 5-min interval (see Dornhaus and Chittka, 2001). This activity is a measure of the foraging motivation of the colony; if many bees leave the nest to search for food, activity is high, whereas during periods of low food availability the activity is very low (Dornhaus and Chittka, 2001). The activity of the colony is measured constantly during a control phase of 30 min and an experimental phase of 60 min. The respective manipulation is carried out during the experimental phase. For the analysis, the average activity during the control phase was compared with the average activity measured in the second half hour of the respective experimental phase. This was to allow for an initial buildup phase of activity under the changed conditions (Dornhaus and Chittka, 2001). Thus, the time intervals compared have an identical duration of 30 min. This paired design controls for any differences in baseline activity between colonies or on different days.

Colony food supply

Experiment 1a: Effect of an active forager

We tested whether food of differing quality would elicit differing responses by the colony. As high-quality food, we used 2 M sucrose in water solution; as low-quality food, we used 0.5 M sucrose solution. In the control phase, no food was available to the bees in the arena. In the experimental phase, one individually marked bee was allowed to collect sucrose solution from a feeder set up in one of the foraging arenas. All other bees only had access to the other arena, which did not contain a feeder; colony activity was measured at the entrance to this arena. The marked forager was offered either high- or low-quality food. The experiment was run 30 times with a total of seven different colonies. In 13 of these runs, a second experimental phase of 60 min immediately followed the first. In each of these two experimental phases, either high- or low-quality food was offered, with the order balanced between runs. To test for a difference between responses with high- and low-quality food sources, only activity from runs with such consecutive experimental phases was compared using a Wilcoxon paired test, which controls for differences between colonies. Activity is thus measured in bees that do not themselves have access to the food source. If their behavior differs between phases during which high- or low-quality sugar solution is collected, this shows that information on food source quality is transmitted to bees in the nest.

Experiment 1b: Forager behavior

Colonies were prepared in the same way as in experiment 1a. A single marked forager was again allowed to forage. The forager's behavior in the nest between foraging trips was filmed (using a digital video camera) and later analyzed for start and duration of unloading, probing of honeypots, occurrence of bouts of fanning, and average speed of movement. We measured speeds by marking the position of a bee on a transparency at every full second and then measuring the step lengths. Foragers often run around on the nest after returning from a new food source (Dornhaus and Chittka, 2001). This behavior might be related to their investment in communicating food availability to nest mates. Particularly the fast, "excited" runs may enhance the efficient distribution of pheromones (Dornhaus and Chittka, 2001). We attempted to quantify these excited runs and separate them from mere probing of pots and other exploration of the nest by measuring the time a forager spent in the nest moving at a speed of more than 40 mm/s. Each forager was only used once with low- and high-quality sugar solution, respectively.

Experiment 1c: Nectar influx without forager

We quantified the bees' reaction to the injection of sugar solution of different concentrations by measuring colony activity in the absence of successfully foraging bees. After the control phase, 100 µl of sugar solution was injected into a honeypot in the nest every 5 min during the experimental phase. A total of 100 µl per 5 min is approximately the amount of sugar solution a forager would have collected in a setup like that in experiment 1a. No food was made available in the arena. This was repeated 5 times each with the high- and low-quality sugar solution (again using 0.5 and 2 M sucrose in water) and another 10 times with two consecutive experimental phases (using 0.5 M sucrose solution in one and 2 M in the other, balanced for order), with a total of five colonies. If the colony's activity depended on the quality of sugar solution injected, that would mean that potential forager bees not only notice nectar influx but also note and react to the quality of the nectar coming into the nest, without having to rely on signals from the active foragers experienced with the food source.

Colony food demand

Experiment 2a: Effect of active forager

The response to a successful forager was measured in colonies with full and empty nectar stores. To guarantee that a colony had full nectar stores, it was fed ad libitum for at least 1 day and tested on the next day. By then, the bees would still have several (5–20) full honeypots in the nest. We made sure, however, that there were always some empty honeypots left, so

that there was enough room to store more honey. The same colonies were also used in the "empty stores" condition. Before colonies were tested as having empty nectar stores, on at least 2 days before the experiment they were only fed as much as they actually used, so that no stores were accumulated. Experiments were started only if no honey was visible in any of the honeypots. The experiment was performed 17 times with full stores and 24 times with empty stores using seven colonies. One individually marked forager was allowed to collect 2 M sucrose solution from a feeder in one arena during the experimental phase. No other bees had access to this food source, but they were allowed to move freely between the nest and the second arena. A significant increase in activity from control to experimental phase would show that bees are alerted to the presence of a profitable food source (Dornhaus and Chittka, 2001). Here, we tested whether this response to the presence of food depended on the amount already stored in the nest (which reflects food demand of the colony).

Experiment 2b: Forager behavior

As in experiment 2a, colonies were manipulated so that they had either full or empty nectar stores. Analogous to experiment 1b, a single marked forager was allowed to visit the feeder and its behavior in the nest filmed on its first return to the colony. This was analyzed in the same way as in experiment 1b.

Experiment 2c: Nectar influx without forager

Again, colonies were tested with full and empty nectar stores. However, no bees were allowed to forage; instead, 100 μl of 2 M sucrose solution was injected into a honeypot every 5 min to mimic nectar influx from a foraging bee. The change in the colony's activity after this manipulation was compared between runs where the colony had either full or empty nectar stores. A difference in the alerting response between these two conditions would indicate that bees have access to information on the current food demand without relying on foragers for the assessment of current food stores in the nest. Forty-eight runs of the experiment were performed, using four colonies.

RESULTS

Colony food supply

Experiment 1a: Information on food source quality is passed from foragers to nest mates

Is the activity of a bumble bee colony modulated according to the quality of the food sources discovered by its foragers? A high-quality food source, in our experiment a feeder with highly concentrated sucrose solution, resulted in a higher colony activity than a low-quality food source, like the feeder with diluted sucrose solution (Wilcoxon signed-rank test: $T = 77.5$, $N = 13$, $p < .05$; Figure 1). The activity during the experimental phase increased significantly relative to the control phase, regardless of quality of the food, but to a higher level if high-quality sugar solution was offered (experiments in which only high quality solution was offered: $T = 36.0$, $N = 8$, $p < .05$; when only low-quality solution was offered: $T = 43.0$, $N = 9$, $p < .05$). Across all experiments, activity was 82% higher than controls when the forager collected low-quality sugar solution, and it was 135% higher if high-quality sugar solution was collected (Figure 1). This means that even if only a low-quality food source was present, some alerting took place, but the alerting effect was stronger for better food sources.

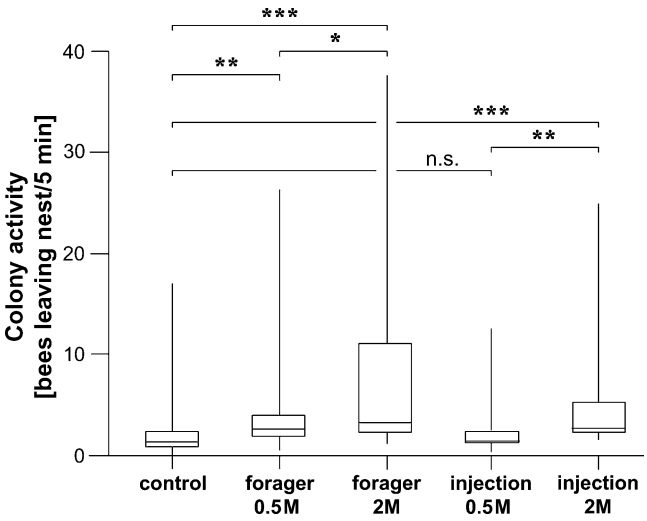

Figure 1
Colony activity in experiment 1 during control phases (no food available) and experimental phases (1a: forager collects high- or low-quality sugar solution and 1c: high- or low-quality sugar solution is injected into honeypots by the experimenter). More bees start foraging when there is an influx of high-quality (2 M) solution. Medians, quartiles, and ranges are shown (sample sizes for columns are 54, 21, 22, 15, 15 experiments, respectively). In this figure, data from all experiments were combined, but the statistical test used only compares paired data of each experimental phase with its respective preceding control phase (i.e., only paired data are used; see text).

Experiment 1b: More excited running after foraging on high quality nectar

After collecting high-quality sugar solution, foragers spent more time on fast running (defined as more than 40 mm/s) than after visiting a low-quality feeder (medians are 2 s versus 0 s; Mann-Whitney U test: $U = 22.5$, $N_1 = 14$, $N_2 = 10$, $p = .004$; Figure 2a). They also deposited their load in a honeypot more quickly (medians are 22 s versus 75 s after entering the nest; $U = 12$, $N_1 = 12$, $N_2 = 6$, $p = .013$). Both of these are still significant when Bonferroni corrected (which requires a $p < .025$ here because data for 2 M experimental phase are also compared with data from phases with full honeypots in section 2b).

Foragers tended to run with higher overall average speed while in the nest after collecting high-quality resolution (medians are 15.7 mm/s versus 13.4 mm/s; $U = 41$, $N_1 = 14$, $N_2 = 10$, $p = .090$; time spent probing pots or unloading excluded), spend less time probing different honeypots (medians are 10 s versus 22 s; $U = 12$, $N_1 = 14$, $N_2 = 6$, $p = .228$), display more bouts of fanning (medians are 3 versus 0; $U = 36$, $N_1 = 15$, $N_2 = 9$, $p = .056$), and spend a longer total amount of time fanning (medians are 3.2 s versus 0.0 s; $U = 40$, $N_1 = 15$, $N_2 = 9$, $p = .097$; Figure 2b), but none of these effects were significant.

Experiment 1c: Bees react differently to nectar injection of differing quality

Injection of high-quality sugar solution into the honeypots resulted in higher activity of colonies than injection of low-quality sugar solution (Wilcoxon signed-ranks test: $T = 55.0$, $N = 10$, $p < .01$, Figure 1). Thus, even without a foraging bee present, bees reacted more strongly to food of higher quality. In fact, it is not clear whether bees in the nest reacted to an injection of low-quality sugar solution at all because the activity did not increase significantly compared to control phases (for experiments in which only low-quality solution was injected: Wilcoxon signed-rank test: $T = 3.0$, $N = 5$, $p = .281$).

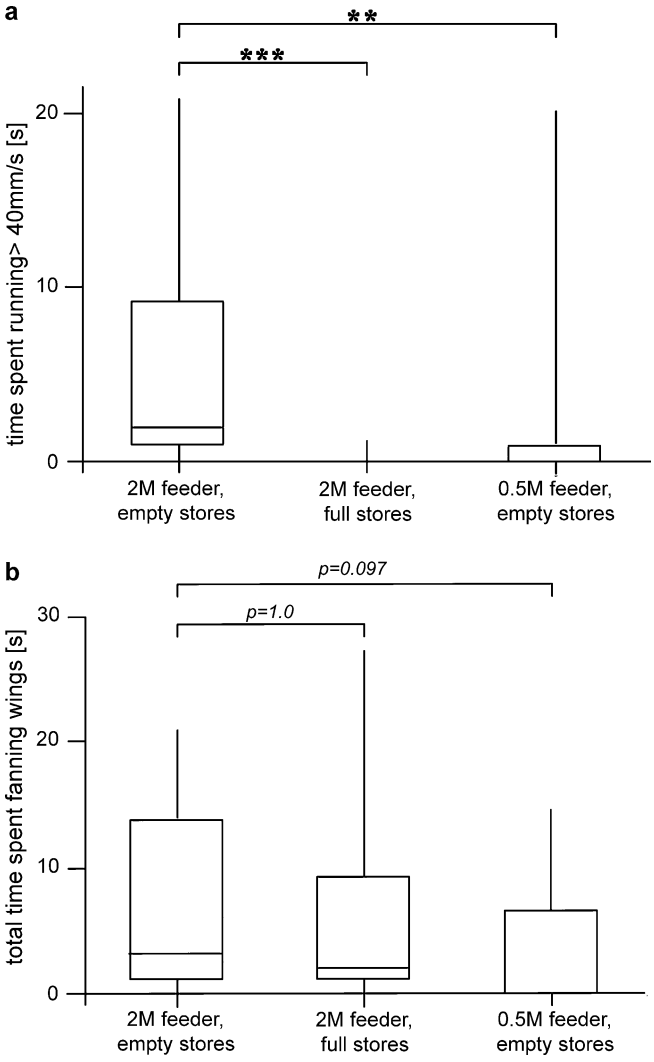

Figure 2
Forager behavior in the nest between foraging trips. Foragers display most excited running (defined here as running at >40 mm/s) when they forage from high-quality (2 M) sugar solution and when nectar stores are empty. Medians, quartiles, and ranges are shown (sample sizes for columns are (a) 14, 9, 10 and (b) 15, 10, 9 foragers, respectively). The figure includes data from all tested foragers, but statistical tests are performed on paired data, controlling for variance between individuals.

In experiments in which only high-quality solution was injected, activity tended to increase compared to controls, but not quite significantly so ($T = 15.0$, $N = 5$, $p = .059$). However, because sample sizes in for both these conditions were small, we combined these data with those from the set of experiments in which both solutions were used in sequence (employing a Bonferroni correction). Injection of low-quality solution still has no effect in the combined data (Wilcoxon signed-rank test: $T = 87.5$, $N = 15$, $p = .125$; the increase in activity corresponds to 6% of overall control activity), but injection of high-quality solution causes a significant increase in activity ($T = 120.0$, $N = 15$, $p < .001$; a Bonferroni correction here requires a $p < .025$; activity is 100% higher than controls). These results are different from experiment 1a, where a forager collecting low-quality sugar solution did cause a significant increase in activity. The stronger reaction of the colony to the presence of a successfully foraging bee indicates that bees extract additional information from the forager.

Figure 3
Colony activity in experiment 2a during control phases (no food available) and experimental phases (a forager is collecting 2 M sugar solution) under conditions of empty or full nectar stores. Bees were only activated by the successful forager if nectar stores were empty. Medians, quartiles, and ranges are shown (sample sizes for columns are 24, 24, 17, 17 experiments, respectively).

Colony food demand

Experiment 2a: Activity increases only when the colony is short on nectar stores

Does the amount of honey already stored have an influence on the occurrence of an alerting response? The activity of the bumble bee colony did not increase from control to experimental phase if it had stored large amounts of honey (Wilcoxon signed-rank test: $T = 84.0$, $N = 17$ experiments, $p = .42$; Figure 3), but it did increase significantly when honeypots were empty ($T = 261.0$, $N = 24$, $p < .0005$). The median difference between activity during the control and experimental phases was 6.3 bees/5 min if the colony had no stores of honey, which corresponds to an increase of 84% in experimental phases, and 1.3 bees/5 min with full honeypots, a 9% increase. The forager's discovery of a food source then did not lead to activation of more bees if there was low food demand in the nest. This could mean that either the forager did not give an alerting signal or that bees in the nest did not react to alerting signals from foragers if a significant amount of honey was already stored. This stronger alerting effect when honey stores were low can also be shown by a direct comparison of the experimental phases with full and empty honey stores (Mann-Whitney U test: $U = 102.0$, $N_1 = 17$, $N_2 = 24$, $p < .01$).

During control phases, that is, if there was no food source available, the activity of colonies did not differ significantly between conditions of low and high nectar stores (Mann-Whitney U test: $U = 175.5$, $N_1 = 17$, $N_2 = 24$, $p = .45$). This means that although colonies with low nectar stores were more sensitive to newly discovered food sources, they did not generally send out more bees to search for food. On the contrary, during control phases, there was a trend to higher activity when stores were already full.

Experiment 2b: Foragers change their behavior depending on nectar stores

When honeypots were empty, foragers displayed more "excited running" behavior than when stores were full. Foragers spent more time running at high speed (medians are 2 s versus 0 s of running at more than 40 mm/s; Mann-Whitney U test: $U = 7$, $N_1 = 14$, $N_2 = 9$, $p = .0003$; Figure 2a)

and moved with a higher speed on average (medians are 15.7 mm/s versus 10.0 mm/s; $U = 13.5$, $N_1 = 14$, $N_2 = 9$, $p = .0018$). They also spent less time probing pots when stores were depleted compared to when honeypots were full (medians are 10 s versus 35 s; $U = 28.5$, $N_1 = 14$, $N_2 = 9$, $p = .029$), although this is not significant when Bonferroni corrected (which requires $p < .025$ in this case).

Foragers tended to unload earlier when honeypots were empty (medians are 22 s versus 41 s after entering the nest; $U = 37$, $N_1 = 14$, $N_2 = 10$, $p = .053$), although this barely missed significance. There was also no significant difference in the number of fanning bouts (medians are 3 versus 2.5; $U = 71$, $N_1 = 15$, $N_2 = 10$, $p = .823$) or the total time spent fanning (medians are 3.2 s versus 2.0 s; $U = 75$, $N_1 = 15$, $N_2 = 10$, $p = 1.0$; Figure 2b).

Experiment 2c: Potential foragers are not alerted by nectar injection if stores are full

If the colony had no stored nectar, injection of sugar solution caused significant activation of potential foragers (Wilcoxon signed-ranks test: $T = 282.0$, $N = 27$, $p < .001$). This was not the case if honeypots already contained large amounts of honey ($T = 137.5$, $N = 21$, $p = .46$; Figure 4).

Figure 4
Colony activity in experiment 2c during control phases (no food available) and experimental phases (2 M sugar solution is injected into honeypots by the experimenter) under conditions of empty or full nectar stores. Bees were only activated by influx of sugar solution if nectar stores were depleted. Medians, quartiles, and ranges are shown (sample sizes for columns are 27, 27, 21, 21 experiments, respectively).

DISCUSSION

The honeypots in a colony of *B. terrestris* bumble bees serve not only to store nectar, they are also an important part of the information distribution system. Potential foragers can collect information on the availability and the quality of currently profitable food sources from honeypots. Bees in the nest detect influx of nectar and if it has a high sugar concentration, they react to it by starting to forage. Moreover, individuals have information about the status of the nectar stores and thus current food demand. If demand is low because most honeypots are filled with nectar, bees do not start to forage in response to nectar influx. If there is no sign of successful foraging by nest mates (as in control phases), activity tends to be lower when honeypots are empty. A possible reason for this is that colonies with low nectar stores try to economize their foraging effort more, that is, only investing energy in food-searching activity if there is some certainty that this would lead to successful foraging.

Potential foragers in the nest thus have information on food availability and demand independently of any forager signals. How do individuals access this information? Individuals may inform themselves about nectar stores by checking particular or all honeypots to monitor nectar influx. Signals from hungry larvae may also convey information on colony food demand (Free, 1987). Bees may perceive demand for nectar by sensing their own hunger level; however, this seems unlikely as individual foragers or bees that have sampled incoming nectar in honeypots would have ingested sucrose and therefore themselves may not be hungry any more.

In addition to the information potential foragers can get by monitoring the honeypots, successful foragers actively alert bees in the nest to the presence of food using pheromone signals (Dornhaus et al., 2003). These signals might serve to alert inactive bees to check the honeypots for new information because now changes in nectar influx are to be expected. The pheromone signal may be modulated by more or less efficient distribution through running and fanning; alternatively, the behavior of excited running itself may constitute an additional signal. The forager signal is graded according to the quality of food sources because the behavior of excited running displayed by foragers is modulated according to sugar concentration. When the forager is collecting low-quality sucrose solution, the forager's signal is necessary for an activation of other foragers to take place; the cue of nectar influx is not sufficient in this case. The running behavior is also modulated according to food demand, with more fast running under conditions of empty nectar stores.

Using both signals (from successful foragers) and cues (from honeypots) potential foragers can thus make informed decisions on whether to start foraging or not, without exposing themselves to the risks and energy costs of sampling foraging conditions and flowers outside the nest themselves. On a colony level, this leads to the regulation of flight activity according to supply and demand for food. Our study only investigates nectar foraging, but these paths of information transfer may be used in the context of pollen foraging as well.

In *B. terrestris*, the honeypots are thus used as a source of information, in addition to signals from other bees. This may be similar in other bumble bee species; the only other species tested in a similar way is *Bombus transversalis*, which also shows an increase in activity after the forager has started collecting sugar solution (Dornhaus and Cameron, 2003). In honey bees (*Apis mellifera*) on the other hand, information about foraging conditions and food demand may be exchanged mainly in direct interactions of foragers and bees in the nest. Foragers stimulate others to start foraging by performing dances in the hive (Frisch, 1967; Seeley, 1995). In nectar foraging, the delay foragers experience before unloading to receiver bees gives the foragers cues on the capacity of the colony to process the incoming food (Ratnieks and Anderson, 1999; Seeley, 1995). Pollen foragers also do not necessarily directly assess the amount of pollen stored by monitoring the pollen cells. Rather, they elicit food samples from the hive bees and judge their protein content. They only start foraging for pollen if they have insufficient protein levels. Active pollen foragers stop foraging for pollen if the protein content of food they receive is already high; if it is very low, they recruit additional pollen foragers by means of dances (Seeley, 1995; Weidenmüller and Tautz, 2002). To decide whether to start foraging, honey bees thus often collect information on supply and demand through direct interactions, "dances," or trophallactic behavior, rather

than surveying contents or changes in the food storage pots themselves.

One reason for these differences in information distribution strategies between bumble bees and honey bees may lie in their different colony sizes. A bumble bee colony always starts with a colony size of 1 (the founding queen). For much of the flowering season, colony sizes are therefore very small (<100). Colony size may then increase to several hundred individuals late in the season but much less if the flowering season is short (up to 50–400, Heinrich, 1979; up to 350 in *B. terrestris*, Goulson, 2003; the maximum size recorded in bumble bees was 2183, in a tropical species, Michener and Laberge, 1954). Honey bees, on the other hand, reproduce by colony fission; natural colony size therefore ranges from a few thousand to about 20,000 individuals (Winston, 1987). In small colonies of bumble bees, the number of potential foragers might therefore often be very low (e.g., Cartar, 1992: median 9 forager bees in three species of New World bumble bees; A. Dornhaus and L. Chittka, personal observation on *B. terrestris*: often <10 bees on any given day, approximately 10% of workers). If workers only spend a few minutes in the nest for each foraging trip of 1 h (Heinrich 1979), and 10 bees are potential foragers, then the average number of foragers in the nest at any one time is less than 1. Potential foragers would therefore have limited access to current information about foraging conditions if they relied on direct forager signals because they would have to wait for an active forager to come back to the nest. A benefit of sampling honeypots is that the information is available at any time. In colonies with a large workforce, the frequency of incoming foragers is likely to be high enough (in a colony with 1000 potential foragers, the same rough calculation as above gives an average of 50–100 active foragers in the nest at any one time), so this problem would not occur.

Second, the nest itself is smaller in bumble bees. This suggests that it might be easier for an individual forager to monitor the food stores in comparison to the situation in a honey bee nest, where a worker would have to patrol a large area to survey the food stores of the colony. Third, bumble bees do not perform trophallaxis (the direct feeding of one individual by another, Moritz and Hallmen, 1986; Liebig et al., 1997), which makes them unable to give food samples directly to nest mates. It also means that, in bumble bees, foragers store their harvest themselves, so there is no group of "receiver bees" as in honey bees. Possibly the evolution of trophallactic behavior enabled honey bees to exchange more information directly, leading to a greater reliance on signaling between active foragers and other bees rather than extracting information from honeypots. If direct information transmission as happens in trophallaxis had been a significant advantage for bumble bees, however, it is surprising that they have not evolved trophallactic behavior. Bumble bees can act as recipients in trophallactic interactions with honey bees (such as when raised with them, A. Dornhaus and L. Chittka, personal observation), and because trophallaxis has evolved in honey bees, stingless bees, and ants convergently (Cameron, 1993; Liebig et al., 1997; Seeley, 1995). It seems an easily obtainable trait).

We have shown that the honeypots in a bumble bee colony are used by potential foragers to collect information on the availability and quality of resources. This implies a blackboard architecture information distribution system, where information is deposited and can be picked up by receivers at any time. Such information is supplemented by direct signals from foragers. In addition, bees only react to such signals or cues when there is demand for food in the colony. Bumble bees can thus obtain extensive information about the current benefits of foraging before exposing themselves to the risky world outside.

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