

Information flow and regulation of foraging activity in bumble bees (*Bombus* spp.)

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Abstract – Communication in the context of foraging in bumble bees has received less attention than in other social bees. Yet, recent studies have revealed that information flow mediates colony foraging activity. The species studied do not recruit to specific locations, but bees can learn the scent of food sources at the nest, which may reduce their search time. Location communication may not confer high benefits to bumble bees. But bees react to nectar influx with increased foraging activity, with high quality food eliciting more activity. This shows that bees recognize and sample freshly collected nectar. If the colony has no demand for food, foraging activity does not increase. Successful foragers distribute a tergal gland pheromone in the nest that also elicits higher foraging activity. Information exchange in the nest thus enables bumble bees to base their decision to forage on demand and the presence and profitability of food.

***Bombus terrestris* / recruitment / social insect / collective foraging / communication**

1. INTRODUCTION

Bumble bees (*Bombus* Latr.) do not show the spectacular recruitment known from honeybees (*Apis* L.) and some stingless bees (Apidae, Meliponini), where a single forager discovering a profitable food source might soon be joined by hundreds of nest mates (Lindauer and Kerr, 1960; Von Frisch, 1967; other articles in this issue). Early studies of bumble bee recruitment therefore concluded that bumble bee foragers are not able to communicate about their finds to nest mates (in *Bombus* (*s. str.*) *terrestris*; *B. (Megabombus) agrorum* (now *pascuorum*), *B. (Pyrobombus) hypnorum*, and *B. (Fervidobombus) atratus*; Wagner, 1907; Kugler, 1943; Jacobs-Jessen, 1959; Esch, 1967; Kerr, 1969). In these studies, a forager was usually trained to an artificial food source and then allowed to for-

age from it, while the experimenter observed whether any other bumble bees would appear at this feeding station. Either no recruits arrived at all (in most of the studies), or not more than at a control feeding station (Dornhaus and Chittka, 1999). The species so far tested are thus not able to communicate locations of food sources to their nest mates.

In spite of this absence of communication about locations of food sources, the bumble bee colony functions as an information centre, where bees obtain information that helps them decide when and where to forage. Like any social insect, bumble bees are under pressure to achieve an allocation of workers to the task of foraging that is adapted to the current availability and demand for food. In effect, there has to be a decision on the level of the colony about whether to activate more foragers or not. This decision emerges from

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the information flow between successful foragers and bees at the nest.

In addition to information about locations of food sources, other foraging-related information is transmitted at the nest, such as food source availability, quality, and scent (at the food source itself there may be some additional communication with scent marks: Cameron, 1981; Stout et al., 1998; Chittka et al., 1999; Goulson, 2003). We discuss what ecological factors may determine the benefits of location communication, and thereby cause honey bees, but not bumble bees, to evolve such communication. We also report evidence that the benefits of location communication in honey bees may be dependent on the spatial aggregation pattern of floral food in the bees' habitat.

2. INFORMATION EXCHANGE ABOUT FOOD SOURCES

2.1. Foraging conditions

To test for transmission of information from foragers to other bees, we deprived all bees from access to any food sources, and then allowed only one individually marked bee to forage from a feeding dish with unscented sugar solution. This was achieved by keeping a colony in the laboratory connected to two foraging arenas; all bees had access to one of the arenas, whereas only the marked forager was allowed to enter the other arena, which contained the food source. Any change in the behaviour of all other bees after the forager started foraging from its exclusive resource then reflects the information passed on to them. Using such a set up, we were able to show that within 30 min after the forager had started foraging, the activity of the colony increased significantly (for *Bombus terrestris*: Dornhaus and Chittka, 1999; for *Bombus transversalis*: Dornhaus and Cameron, 2003). Activity was defined as the number of bees leaving the nest per time interval; its increase was due to both more individuals starting to search for food and the same bees increasing their effort, by patrolling the arena in shorter intervals (Dornhaus, 1999). On the colony level, this means that the number of bees allocated to foraging is adjusted to the current



Figure 1. When nectar stores were low (black bars), a single forager who discovered a new food source was able to stimulate many inactive bees to start looking for food. This is reflected by an elevated activity (measured in bumble bees leaving the nest per 5 min) after the forager had started bringing in nectar ("experimental phase"). If the colony still had full honeypots, activity remained unchanged (white bars). (n gives the number of experiments) (Dornhaus, 2002).

foraging conditions, with the first bee discovering profitable food sources triggering an increase in search effort that may lead to the entire foraging force being mobilised within an hour of the discovery.

The colony's rise in activity depends on the concentration of the sugar solution, and thus the quality of the discovered resource. When the forager was allowed to feed from a food source that contained 0.5M sucrose solution, activity did not increase as much as it did when the forager was fed 2M sucrose solution. This indicates that bees do not transmit an all-or-nothing signal, but instead the amount of activation depends on the quality of food sources discovered (Dornhaus, 2002). It also depends on the amount of honey stored in the colony. When the experiment was repeated after colonies had been fed ad libitum for a few days (and thus had several full honey pots), no increase in activity after a forager discovered a new food source was observed (Fig. 1; Dornhaus, 2002).

2.2. Scent of food sources

Using a similar set up, we tested whether the scent of a food source discovered by the forager could be learned by bees in the nest.

Again, only one marked forager was allowed to feed from an artificial food source, this time containing scented sugar solution. In the other arena, three feeders were set up containing scented water, each feeder with a different scent. One individual at a time, the bees leaving the nest were then allowed into this arena, to test for their preferences among the three scents. They significantly preferred the scent that was currently collected by the forager (Dornhaus and Chittka, 1999). Naïve foragers could thus learn the scents of food sources currently harvested by nest mates, and use this information to select profitable flower species to forage from by searching for these scents. Alternatively, experienced foragers may be alerted to the re-appearance of profitable food sources, and may be able to return to known food patches of the corresponding scent. The latter form of use of scent information has previously been suggested for honey bees (Wenner and Johnson, 1966; Von Frisch, 1967; Wells and Rathore, 1995).

3. MECHANISMS OF INFORMATION FLOW

How does the information about foraging conditions get transmitted from a forager to other bees in the nest? Foragers could be producing direct signals, serving to communicate this information to their nest mates, or bees in the nest could be using cues to identify whether other bees were currently foraging successfully. It turns out that both mechanisms are at work.

3.1. Pheromone signal and behaviour

Foragers produce a pheromone with glands located in the abdominal tergites, which causes other bees to leave the nest to start foraging. We used two different approaches to show the involvement of such a pheromone signal. In one study, the information that a profitable food source has been discovered was transmitted from one colony to another if air flow between the two nests was possible, but not if this air flow was interrupted by a sheet of plastic wrap (Dornhaus and Chittka, 2001). Secondly, a hexane extract produced from the last three abdominal tergites but not

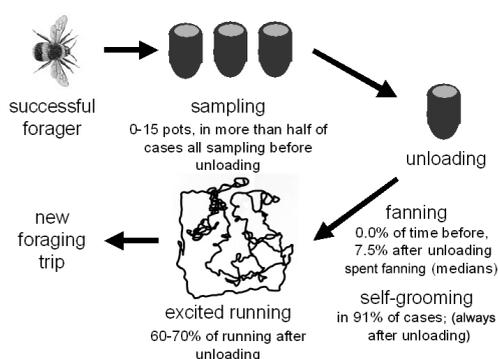


Figure 2. Bumble bee behaviour in the nest between two consecutive foraging bouts. Total time in the nest can be as little as 13 s, but particularly after the first foraging bouts after discovering a food source it can be as long as 10–15 min (Dornhaus and Chittka, 2001).

an extract produced from other parts of the cuticle or from head glands elicited increased activity in a bumble bee colony (Dornhaus et al., 2003). Part of the activation after the discovery of a profitable food source thus is caused by a pheromone distributed by the forager. Foragers also show a conspicuous behaviour after returning from a food source, particularly in the first trips, that might serve to aid the efficient distribution of the pheromone (Fig. 2). They excitedly run around on the nest for extended periods (up to 15 minutes; Dornhaus and Chittka, 2001), fanning their wings in short bouts. The number of fanning bouts displayed seems to depend on the quality of the food source, with higher sugar concentration causing more fanning bouts (Dornhaus, 2002). Foragers are not followed by other bees as they are performing these runs, which indicates that the runs in themselves, as motor behaviours, are not attended to by nest bees (Dornhaus and Chittka, 2001). Their communicative function may therefore be limited to the improved distribution of the pheromone signal (although foragers may also produce acoustic signals during these runs, pers. obs.; Oeynhausen and Kirchner, 2001).

This kind of communication about food sources, i.e. using a pheromone to inform nest mates about good foraging conditions, has not been demonstrated in other social bees. Both honey bees and stingless bees are known to

produce signals that increase the activity of nest mates, particularly after discovering profitable food sources. However, these usually consist of motor signals, like the “dances” in honey bees and “excited movements” in stingless bees, both of which also involve acoustic signals (Lindauer and Kerr, 1960; Esch, 1967; Von Frisch, 1967; Nieh, 2004). Even in ants and wasps, similar fast motor behaviours or “dances” have been observed and interpreted as serving to activate nest mates for foraging (Hölldobler and Wilson, 1990; Richter, 2000). It remains so far untested whether these movement patterns in species other than bumble bees are also accompanied by pheromone signals. This seems a promising line for further research.

3.2. Monitoring of honey pots

Signals from the forager are not the only means by which information about current foraging conditions is available to bees in the nest. Even without a forager present, injection of sugar solution into honey pots shows that bees monitor nectar stores and react to an influx of nectar by increasing foraging activity (Dornhaus and Chittka, 2001). As if a forager was collecting this nectar, the increase in activity also depends on sugar concentration (Dornhaus, 2002). Bumble bees in the nest must thus monitor and sample contents of honey pots and recognize whether nectar has just been collected. This raises the question of how they distinguish between older stored honey and freshly collected nectar.

One possibility is that fresh nectar can be distinguished chemically from honey. Bumble bees process their collected nectar, but this has been very little studied (Crane, 1991). We sampled honey from three colonies of *Bombus terrestris*, which were kept in the laboratory and fed with pollen and Apiinvert (a commercially available bee food) (Dornhaus and Chittka, unpublished data). Honey samples were taken from honey pots on three different days, and analysed at the Institute for Apidology in Celle (Niedersächsische Landesanstalt für Bienenkunde, Celle, Germany). Samples were tested for enzyme activity (glucose oxidase and invertase) and concentration of prolin (an amino acid) with standard methods (Schepartz and Subers, 1964, Deutsches Insti-

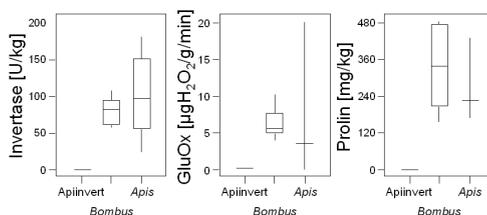


Figure 3. The results of the chemical analysis of *Bombus terrestris* honey are mostly within the range known from honey bees, *Apis mellifera* (mean values, quartiles and ranges; Apiinvert, *Bombus*: Dornhaus and Chittka, unpublished data, Apis: von der Ohe and von der Ohe, 1996; Oddo et al., 1999).

tut für Normung, 1998, 2002). Glucose oxidase, which limits microbial growth in honey (Weston, 2000), and invertase, which breaks down disaccharides into monosaccharides (Oddo et al., 1999), as well as prolin (an amino acid) were found in the bumble bee honey in similar levels as is known from honey bee honey (Fig. 3). We tested a sample of Apiinvert (the food given to colonies in this study) using the same methods as a control. It did not contain measurable amounts of prolin, and only very low levels were recorded in enzyme activity tests (Inv: 0.5 U/kg; GluOx: 0.1 µg H₂O₂/g/min). In honey bees, all of these substances are produced in the hypopharyngeal gland (von der Ohe and von der Ohe, 1996; Oddo et al., 1999; Weston, 2000). Their presence in bumble bee honey indicates the treatment of honey with gland secretions, which is why they are used as measures for honey ripeness and freshness in analysis of commercial (honey bee) honeys. *Bombus terrestris* thus seems to treat nectar with similar glandular secretions as honey bees do. It is therefore possible that bees in the nest can monitor influx of nectar by sampling honey pot contents and recognizing the presence of unprocessed nectar. However, there is clearly a need for more studies investigating the exact mechanisms by which bees in the nest select storage pots to monitor and how they recognize freshly collected nectar. More chemical analysis might also reveal which glands are used in treatment of nectar, and whether bumble bees react to the presence or absence of such chemical components. Alternatively, they might measure the actual volume of honey stored.

That individual bees monitor the entire honey stores of their colony to measure nectar influx is conceivable in bumble bees, since there is not as much storage area as in species with larger colony sizes, like honey bees. Most temperate bumble bee species live in small, annual colonies that are founded by a single queen in the spring and grow to a size of up to a few dozen to a few hundred workers by the end of the growing season (Heinrich, 1979; Laverty and Plowright, 1985). Since the colony does not have to survive an extended period (winter) without foraging, honey stores need to support the colony only for a few days of bad weather (Allen et al., 1978; Heinrich, 1979). The average worker/honey pot ratio is fairly constant at 2.1 ± 0.5 (personal observation of 10 colonies with 24 to 113 workers), but only a few of these may be used for storage of new incoming nectar at any one time. In addition, bumble bees do not show trophallaxis (the direct feeding of one adult individual by another), and foragers unload their collected nectar directly into honey pots. Foragers and potential foragers thus regularly access the storage area, and there is no spatial separation of honey pots from the rest of the nest. Honey pots are therefore an easy, yet efficient way of storing information in a shared environment, rather than relying on direct interaction of individuals for information exchange.

3.3. Direct and indirect information transmission

Information about foraging conditions is thus received by *Bombus terrestris* in the nest through two channels. Foragers give pheromone signals when they have discovered profitable food sources, probably aiding the distribution of these pheromones by running and fanning in the nest. Secondly, nest bees are able to collect information on the availability and quality of food sources from the nectar stores, by monitoring and sampling honey pot contents. These two sources of information may complement each other. For example, the pheromone may prompt bees to check the honey pots for samples of newly collected nectar. However, each of the two is by itself sufficient to cause an increase in colony foraging activity. Both ways of distributing information thus contribute to the colony's ability to regu-

late the allocation of individuals to foraging according to supply and demand.

4. WHY NOT LOCATION?

In bumble bee species so far tested, foragers seem not to be able to recruit nest mates to a particular profitable food source. Through scent learning, bees mobilized by the forager might be able to pick out profitable flower species, but they do not arrive at the same location as the forager (Dornhaus and Chittka, 1999). Why is this so? Would it not be advantageous for a bumble bee colony if successful foragers were able to directly guide or point recruits to the source they have discovered? Surprisingly, the answer may be "no". The potential benefits of recruitment might be so low that they do not outweigh the costs (of energy and time investments) or do not confer a sufficient selective advantage to drive the evolution of such a communication system.

The benefits of recruitment to specific locations could be influenced by several factors. For example, small colony size has been hypothesised to decrease benefits of recruitment (Von Frisch, 1967). However, there are no published studies investigating the influence of colony size on the benefits of food recruitment. Another factor may be more crucial for the evolution of location communication: spatial resource distribution (Visscher and Seeley, 1982; Hölldobler and Wilson, 1990; Sherman and Visscher, 2002; Dornhaus and Chittka, 2004). If resources were densely and evenly spread throughout the foraging range and of equal quality, recruitment to a specific location would not improve foraging success or reduce search time. To the contrary, it might increase intra-colony competition. This may be the case in uniform environments where a large number of plants come into flower within a relatively short time. If, on the other hand, there are few, widely spaced resources of highly variable quality, finding one of these resources without prior information would require an immense search effort.

To assess the role of spatial resource distribution, benefits of location communication have to be quantified in different habitats with different resource distributions that resemble

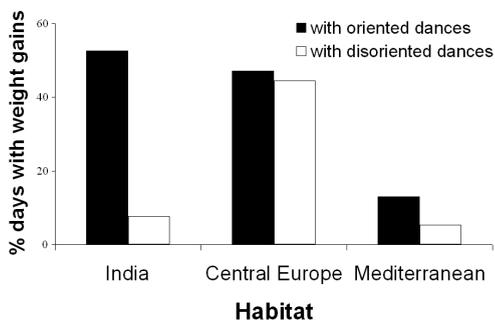


Figure 4. Relative frequency of days with weight gain, i.e. days of successful foraging, in honey bee colonies with and without ability to communicate location of food sources in waggle dances. A significant effect of dance manipulation was found in the tropical habitat, where without dance communication, colonies rarely ever gained weight. No so in the two temperate habitats, where bees forage equally well with and without communication about location of food sources ($n = 2$ colonies per habitat, at least 10 days per colony in each condition) (Dornhaus, 2002; Dornhaus and Chittka, 2004).

those encountered by bees during their evolution. We have quantified the improvement in foraging success through recruitment to locations in manipulated honey bee hives in three locations (Dornhaus, 2002; Dornhaus and Chittka, 2004). Hives were brought into a horizontal position, in which the waggle dance, the communication system of honey bees, loses its location information unless bees are allowed to orient using the sun's location. Foraging success of hives deprived of the means to recruit to specific locations was not significantly affected in two European habitats (an agricultural habitat in Germany and a Mediterranean, undisturbed habitat in Spain), but in a dry forest habitat in Southern India, the colonies lost the ability to efficiently exploit the richest food sources (Figs. 4 and 5). This difference between the habitats indicates that environmental factors, such as resource distribution, may determine the magnitude of benefits from recruitment. In some environments, communicating location may not confer significant benefits to the colony. This is supported by another study using similar methods, in which recruitment was shown to improve foraging success at specific times of the year

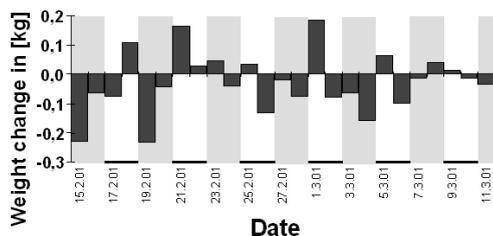


Figure 5. Example of weight changes of one honey bee colony in the experiment in India (dry tropical forest; shaded areas mark periods with disoriented dances). There is high day-to-day variability in nectar intake of the colony. The most successful foraging days are always within periods with oriented dances, which probably means that high-quality food sources could only be exploited efficiently if location communication was possible (Dornhaus, 2002).

only (Sherman and Visscher, 2002). Bumble bees have evolved in temperate habitats, which may be dominated by relatively evenly distributed food sources (Heinrich, 1979; Walther-Hellwig and Frankl, 2000). This might explain why they do not have a communication system that allows recruitment to specific locations.

Bumble bees are not the only social bees which lack a system to communicate locations of food sources. Some stingless bee species have also been described as possessing the ability to alert nest mates after discovering food, without being able to recruit them to its location (*Trigona angustula*, *T. iridipennis*: Lindauer and Kerr, 1960; Esch et al., 1965; Kerr, 1969; for a more recent review see Nieh, 2004). Stingless bees live in habitats very different from those of most bumble bees (Kerr, 1969; Heinrich, 1979; Goulson, 2003), and indeed there is high variation among stingless bees both in recruitment strategies and habitat use (Nieh, 2004). Systematically assessing whether there are any correlations of resource distribution and recruitment system in stingless bees is likely to lead to better understanding of the role of resource distribution for recruitment evolution. It is likely that a number of other factors contribute to the benefit of recruitment to specific locations, for example intra- and interspecific competition (Johnson and Hubbell, 1975). Once more information is available on the phylogeny of the stingless bees and bumble bees (Lockhart

and Cameron, 2001; Nieh, 2004), mapping recruitment as well as ecological characters onto the phylogenetic tree will shed light on the evolution of communication traits as well as possible selective pressures conducive to the evolution of location-specific recruitment.

5. CONCLUSION

In the process of foraging, a bee gathers not only food but also information about food sources and foraging conditions. Currently “unemployed” foragers might benefit from receiving such information for two reasons: it will enable them to judge current expected foraging success, which may influence their decision whether to start foraging at all; and secondly, it helps naïve bumble bees locate the most profitable flower species using scent information, increasing the amount of food they are likely to collect per foraging trip.

The decision whether to start foraging reflects a trade-off between the benefits, i.e. expected energy returns, and the costs, particularly the risks encountered when leaving the shelter of the nest. Predators, parasites and bad weather can be encountered during a foraging trip and contribute to high forager mortality (e.g., Allen et al., 1978; König and Schmid-Hempel, 1995; reviewed in Heinrich, 1979; Plowright and Lavery, 1984; Seeley, 1985a; Goulson, 2003). Optimal allocation of workers to foraging may mean not foraging at all, if expected returns are low and the risk of losing foragers high. On the other hand, a large proportion of the colony’s workforce may be employed as foragers to exploit a rich food source (Seeley, 1985a, 1995; O’Donnell et al., 2000), especially during times of high demand for food (Jacobs-Jessen, 1959; Cameron, 1989; Cartar, 1992; Plowright et al., 1993). This requires individual bees to make realistic estimates of the current expected benefits of foraging. These, however, can change rapidly and frequently (Seeley, 1995; see also Fig. 5). Nectar yield and sugar concentration vary widely between flower species, and also within species over time and space (e.g., Kleber, 1935; Heinrich, 1976; Chittka and Schürkens, 2001; Goulson, 2003). Weather conditions also vary within short periods, and can add to the energy costs of foraging or

make foraging impossible (Comba, 1999). In the face of such variability, and the costs associated with collecting information on foraging conditions, information exchange about current expected foraging success is crucial to enable bees to decide whether to start foraging or not.

Such information on the foraging success of nest mates is picked up by bumble bees both directly from behaviour of the foragers and indirectly from changes in nectar stores. The nest thus functions as an information centre (Brown, 1988; Seeley, 1985b), where information on presence and profitability of food sources is stored and unsuccessful or unemployed foragers can learn the scent of profitable food sources. Such use of a shared environment as a collectively used information pool may facilitate efficient communication especially in species with smaller colonies, because it enables individuals to transmit information without having to directly encounter one another. One might speculate that primitive social bees first evolved the capacity to be stimulated by nectar influx (caused by successful foraging and thus correlated with good foraging conditions), and then to anticipate this nectar influx by recognizing successful foragers, using cues like fast movement or flower odours. Once bees attend to forager behaviour, foragers may in turn have been selected to exaggerate movements or display other signals which would make them more easy to recognize as being successful, leading eventually to the “excited runs” and pheromone signals displayed by bumble bees and other social bees (Lindauer and Kerr, 1960; Von Frisch, 1967; Nieh, 2004). Since scent learning and fast or exaggerated movements seem to occur in all stingless bees and bumble bees, it is likely that these behaviours were already present in their last common ancestor (Dornhaus and Chittka, 2001; Dornhaus and Cameron, 2003; Nieh, 2004).

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Résumé – Flux d'informations et régulation de l'activité de butinage chez les bourdons (*Bombus* spp.).

La communication concernant les sources de nourriture a fait l'objet de bien moins d'attention chez les bourdons (*Bombus* Latr.) que chez les autres abeilles sociales. Des études récentes ont pourtant montré que les bourdons possédaient un répertoire comportemental riche et subtil pour échanger des informations concernant les conditions de butinage (Dornhaus et Chittka, 2001). Les espèces étudiées ne recrutent pas pour des lieux définis, mais des informations concernant la présence et la rentabilité des sources de nourriture est disponible dans le nid pour les butineuses potentielles. Les bourdons peuvent aussi apprendre dans le nid l'odeur des sources de nourriture, ce qui peut réduire considérablement le temps de recherche lors du butinage (Dornhaus et Chittka, 1999).

Dans le nid, les bourdons contrôlent les variations des réserves de nectar et réagissent à l'afflux de nectar en augmentant leur activité de butinage. On a pu le montrer en manipulant les réserves de nectar. Un afflux de nourriture de grande qualité (ayant une teneur en sucres élevée) suscite une plus grande activité. Ceci prouve que les bourdons reconnaissent et inspectent dans les pots à miel le nectar fraîchement récolté (Dornhaus, 2002). La sensibilité des bourdons à l'afflux de nectar dans le nid dépend néanmoins de la quantité de nectar déjà stockée. Lorsque les réserves de miel sont pleines, aucune nouvelle butineuse n'est mobilisée (Fig. 1 ; Dornhaus, 2002).

Les butineuses utilisent aussi, outre ce transfert indirect d'informations, des signaux directs. Lorsqu'elles rentrent à la colonie après avoir découvert une source de nourriture rentable, les butineuses présentent un comportement caractéristique : elles courent ici et là sur le nid, visiblement excitées, et font bourdonner leurs ailes (Fig. 2 ; Dornhaus et Chittka, 2001). Elles distribuent aussi une phéromone, produite dans la glande tergaire abdominale, qui déclenche une augmentation de l'activité de butinage (Dornhaus et al., 2003). L'échange d'informations dans le nid permet ainsi aux bourdons de fonder leur décision de butiner sur la présence et le degré de rentabilité des sources de nourriture et donc sur l'attente d'un butinage fructueux.

Ces diverses voies de flux d'informations permettent à une colonie de bourdons de réguler son activité de butinage en fonction de l'offre et de la demande de nourriture. Lorsque les conditions de butinage sont bonnes, le nombre de bourdons qui butinent s'accroît grâce aux signaux phéromonaux des premières butineuses qui rentrent chargées de nectar et grâce à la perception de l'afflux de nectar dans les pots à miel par les ouvrières d'intérieur. Lorsqu'il y a peu de nourriture disponible, une faible activité économise l'énergie et réduit la perte d'ouvrières ; mais lorsque les conditions s'améliorent, les butineuses peuvent être rapidement mobilisées.

Il se peut que la communication du lieu n'apporte pas de grands avantages aux bourdons. Nous l'avons testé en manipulant des ruches d'abeilles domestiques et n'avons pu établir une influence de la communication du lieu sur le butinage que pour l'un des trois habitats (Fig. 3 ; la figure 4 montre la forte variabilité du résultat du butinage avec et sans communication du lieu). Les avantages apportés par la communication du lieu, et donc la pression de sélection sur le système, peuvent donc être extrêmement variables et dépendre de facteurs tels que la répartition spatiale et temporelle des sources de nourriture.

Bombus terrestris / recrutement / butinage collectif / communication

Zusammenfassung – Informationsübertragung und Regulation der Fouragieraktivität in der Hummelkolonie.

Die Kommunikation über Futterquellen bei Hummeln ist wesentlich weniger untersucht als bei Honigbienen. Unsere Studien in letzter Zeit haben jedoch gezeigt, dass Hummeln ein Repertoire von Verhaltensweisen besitzen, die ihnen ermöglichen, Informationen über Futterquellen auszutauschen (Dornhaus und Chittka, 2001). Die untersuchten Arten rekrutieren zwar nicht zu spezifischen Orten, aber Hummeln im Nest haben Zugang zu Informationen über das Vorhandensein und die Profitabilität von Futterquellen. Sie lernen ausserdem den Duft des eingetragenen Futters, was ihnen vermutlich hilft, ihre Suchzeit beim Fouragieren zu reduzieren (Dornhaus und Chittka, 1999).

Die Hummeln verfolgen im Nest den Stand der Nektarvorräte. Die Fouragieraktivität erhöht sich, wenn Nektar hinzukommt, ob es sich um eine erfolgreich fouragierende Hummel handelt oder um experimentell hinzugefügten Nektar. Hochkonzentrierte Zuckerlösung löst dabei mehr Aktivität aus als solche mit niedriger Zuckerkonzentration. Das bedeutet, dass Hummeln den frisch hinzugekommenen Nektar in den Honigtöpfen erkennen und prüfen (Dornhaus, 2002). Wie empfindlich die Hummeln auf eingetragenen Nektar reagieren, hängt ausserdem von den bereits vorhandenen Nektarvorräten ab. Ist bereits viel Honig vorhanden, fliegen keine zusätzlichen Sammlerinnen aus (Abb. 1; Dornhaus, 2002).

Neben dieser indirekten Informationsübertragung nutzen erfolgreiche Sammlerinnen auch direkte Signale. Nach der Rückkehr von einer profitablen Futterstelle zeigen die Hummelsammlerinnen ein charakteristisches Verhalten, in dem sie scheinbar aufgeregt im Nest umherlaufen und oft mit den Flügeln schwirren (Abb. 2; Dornhaus und Chittka, 2001). Dabei produzieren sie in Drüsen an den Abdominaltergiten ein Pheromon, das höhere Fouragieraktivität bei ihren Nestgenossinnen auslöst (Dornhaus, 2003). Informationsaustausch im Nest ermöglicht Hummeln also, ihre Entscheidung zum Futtersammeln von guten Sammelbedingungen und

der Präsenz profitabler Futterquellen, und damit von einem zu erwartenden Erfolg des Fouragierens, abhängig zu machen.

Der Informationsaustausch im Hummelnest führt zu einer Anpassung der Fouragieraktivität je nach Angebot an und Nachfrage nach Nektar. Bei guten Sammelbedingungen steigt die Anzahl der ausfliegenden Hummeln, ausgelöst sowohl durch die Pheromonsignale der ersten erfolgreichen Sammlerinnen als auch den Anstieg der Nektarvorräte. Ist dagegen ein geringes Nektarangebot vorhanden, führt eine geringe Aktivität der Hummelkolonie dazu, dass Energie gespart wird und die Arbeiterinnen keinen unnötigen Risiken ausgesetzt werden. Wenn die Bedingungen sich ändern, können Sammlerinnen schnell wieder mobilisiert werden. Ebenso führt ein geringer Bedarf an Nektar zu einer Einschränkung der Mobilisierung von Sammlerinnen.

Möglicherweise würde ein zusätzlicher Austausch über den Ort von Futterquellen bei Hummeln nicht zu höherem Sammelerfolg führen. Wir untersuchten den möglichen Anstieg im Sammelerfolg durch Ortskommunikation bei experimentell manipulierten Honigbienenstöcken. Nur in einem von drei Habitaten konnte ein Effekt der Ortskommunikation auf Sammelerfolg festgestellt werden (Abb. 3; Abb. 4 zeigt die hohe Variabilität im Sammelerfolg mit und ohne Ortskommunikation). Die Vorteile der Ortskommunikation, und damit der Selektionsdruck, ein solches System zu entwickeln, sind daher vermutlich sehr variabel, und hängen von Faktoren wie räumlicher und zeitlicher Verteilung von Futterquellen ab.

***Bombus terrestris* / Rekrutierung / soziale Insekten / kollektives Sammelverhalten / Kommunikation**

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